Vol. 81 JULY-AUGUST 1954 No. 4

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Bulletin of the Torrey Botanical Club

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Published for the Club bi-monthly
by
THE BUSINESS PRESS, INC.
N. QUEEN ST. AND McGOVERN AVE.
LANCASTER, PENNSYLVANIA

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The subscription price of the Bulletin of the Torrey Botanical Club (including Torreya), is $9.00 a year except to active members of the Club. The annual membership dues covers a year's subscription to the Bulletin.

Entered as second-class matter October 8, 1940 at the post office at Lancaster, Pa., under the Act of March 3, 1879. Accepted for mailing at the special rate of postage provided for in the Act of February 28, 1925, embodied in Paragraph (d-2) Section 34.40 P. L. & R. of 1948.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 81, NO. 4, PP. 271–287 JULY, 1954

DEVELOPMENT OF THE SEED COAT OF LIMA BEAN (PHASEOLUS LUNATUS L.)[1]

CLARENCE STERLING

During the course of a study of factors associated with the maturation of lima beans used for freezing, it seemed desirable to investigate histological as well as physiological changes which occurred during seed development. Such an investigation could yield data instrumental in assessing bean maturity and provide as well basic information on developmental processes in an important leguminous seed. The first phase of this research deals with histogenetic aspects of seed coat ontogeny.

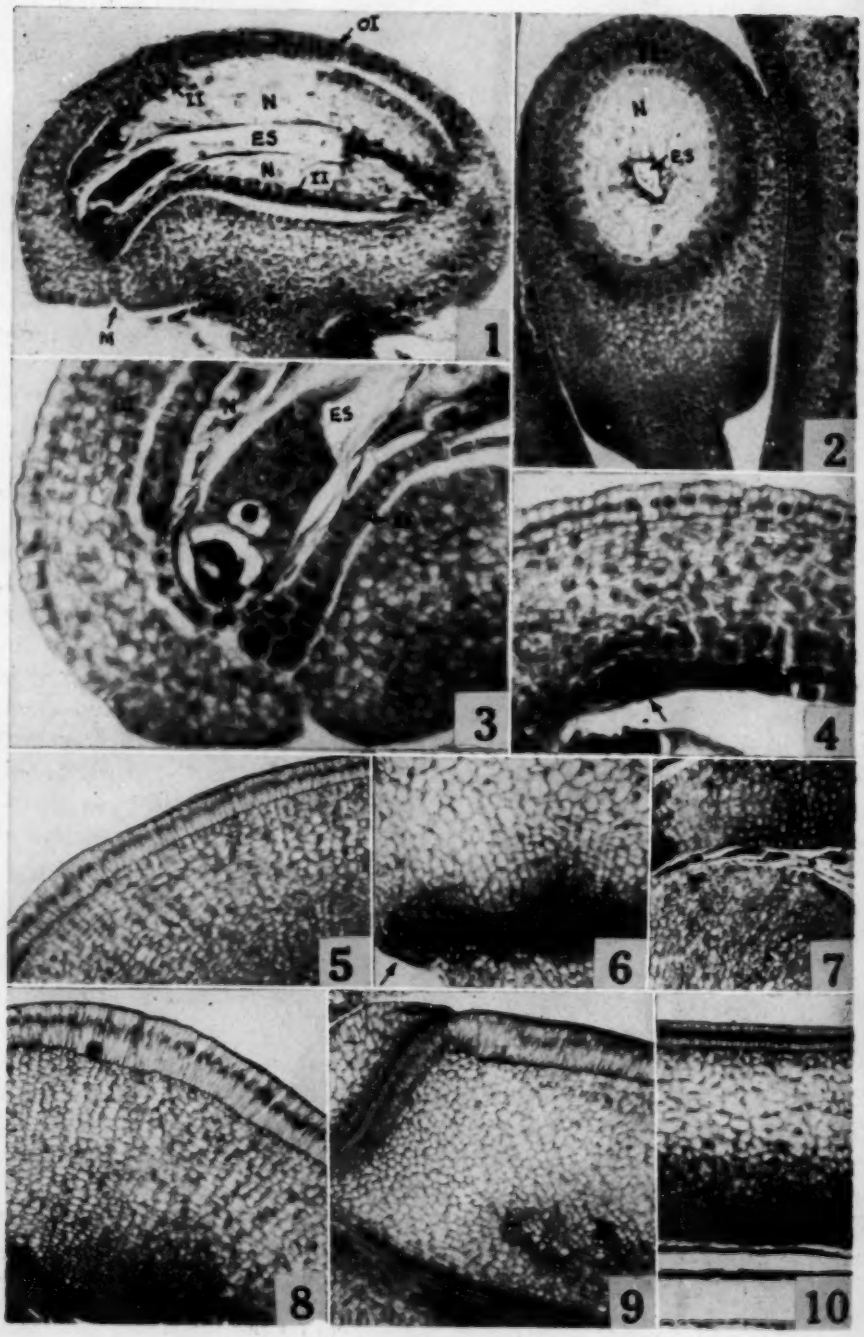
The comparative anatomy of the mature seed coat in legumes has been intensively explored by Corner (1951), Chalon (1875), Harz (1885b), Mattirolo and Buscalioni (1889, 1892), Pammel (1899), and Pitot (1935a), to name a few. Specific details of the structure of the seed coat of lima bean and other species of *Phaseolus* are available in the works of Harz (1885b), Tschirch and Oesterle (1900), and Winton and Winton (1935). However, few histogenetic studies have been made of seed coat development in the Leguminosae. Haberlandt (1877) dealt with details of seed coat ontogeny in *Phaseolus vulgaris*, the common bean. Brandza (1891) also considered seed coat development in various plants, including *P. vulgaris* briefly among legumes. Apparently he was unaware of Haberlandt's earlier work on this subject. Some features of ontogeny in the seed coat of *P. multiflorus* are described by Mattirolo and Buscalioni (1892). With the added exceptions of Pitot's (1935b) short comparative account of legume seed coat development, Pfaefflin's (1897) investigation of the ontogeny of the "tracheid island" and the "chilarion" in *P. vulgaris*, and Reeve's (1946b) study of sclereid development in the seed coat of *Pisum*, most descriptions of seed coat ontogeny in legumes are fragmentary. No studies have been made of the development of the testa of the lima bean.

Materials and methods. Plots of Henderson Bush (thin-seeded) and Evergreen (baby potato) lima beans were provided by the Associated Seed Growers' Station in Milpitas, California. Full bloom in both varieties occurred on July 31, 1951. On this date, all previously set pods were removed by hand. Specimens were collected at 2–3 day intervals from July 31 to September 14. On the latter date, the pods were becoming thin and papery, and the beans were starting to shrink and harden.

For histological study, young pods and ovules were immersed in a for-

[1] Dr. B. R. Wagnon graciously prepared the slides for this study.

[THE BULLETIN for May–June, 1954 (81: 169–269) was issued May 14, 1954]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malin-acetic acid-alcohol mixture (Johansen, 1940) and preserved therein. Dehydration was accomplished with a graded ethanol-xylol series, following which the material was embedded in "Tissuemat." After being cut at 10 μ, sections were stained with tannic acid-ferric chloride, safranin, fast green, and crystal violet for the most part. However, other stain combinations were sometimes used.

Terminology. In order to clarify the description of developmental processes, the following terms of orientation will be used with reference to the campylotropous seed:

Median plane—the plane passing through funiculus, micropyle, and chalaza, perpendicular to the placental surface.

Transverse plane—any plane perpendicular both to the median plane and to the placental surface.

Frontal plane—any plane parallel to the placental surface, hence perpendicular both to the median and transverse planes.

Anterior—at or to the stylar end of the ovule.

Posterior—at or to the receptacular end of the ovule.

Dorsal—at or to the side of the ovule farthest from the placenta.

FIGS. 1–10. Placenta toward bottom of page in all unless otherwise noted. FIG. 1. Median section of Evergreen ovule at time of flowering. ×130. FIG. 2. Transverse section through mid-region of Henderson Bush ovule at flowering. Megagametophyte (embryo sac) in center of ovule surrounded by light nucellar tissue. Dark-staining tissue of outer integument (derived from O_4 and O_5—see text) surrounds somewhat lighter tissue of inner integument. Note two procambial strands placed just ventrally of the nucellar region, at either side of median plane. ×130. FIG. 3. Median section of micropylar region of Evergreen ovule at fertilization. Note disintegrating nucellus just inside the biseriate inner integument. ×308. FIGS. 4–10 of Henderson Bush. FIG. 4. Dorsal portion of micropylar region in median section 2 days after flowering. Start of pronounced coaxial growth. Notable radial elongation in outer epidermal cells. Dark mass at arrow is disintegrating region of rim of inner integument. ×308. FIG. 5. Anterior region of micropylar rim (towards upper left) in median section at 4 days. Rather large ovule of this stage, with pronounced "Springbrunnen" meristem. ×130. FIG. 6. Transverse section at funiculus-integument boundary at 3 days. Arillate growth of funiculus at arrow. Note coaxial divisions in frontal plane in median region, which predestine the tracheid island. ×149. FIG. 7. Median section of 3 day ovule. Below young embryo is mound of tissue being formed into rim which will enclose future radicle pocket at left. Embryo is thus forced into a curved orientation of hypocotyl during growth. ×149. FIG. 8. Median section of anterior micropylar rim (upper right) at 10 days. Mitotic activity has ceased in these cells and in the palisade cells. ×92. FIG. 9. Median section of strophiolar region at 13 days. Placenta at top of page. Vascular bundle to ovule at lower left. Arillate extension of funiculus adjoining palisade cells at upper left. Active elongation of the subepidermal cells to raise the strophiole has not begun yet. ×92. FIG. 10. Median section of dorsal portion of seed coat at 20 days. At bottom of photo are epidermal cells of cotyledon, then isolated strip of endosperm cells, followed by disintegrating inner stratum of inner integument. In outer integument, inner zone of cells has reached maximum radial extent by mitotic activity. Cells of palisade layer are still only slightly elongated. ×149. ES = embryo sac; II = inner integument; M = micropyle; N = nucellus; OI = outer integument.

Ventral—at or to the side of the ovule nearest the placenta.
Lateral—at the surfaces of the ovule on either side of the median plane.
Periclinal or tangential—parallel to a free surface.
Anticlinal—perpendicular to a free surface.

Integument structure at flowering. Although the Henderson Bush variety was studied most intensively, the following details of structure and development are common to both varieties. In each ovary there are from two to four ovules which are campylotropous on a broad funiculus. The micropyle is located at the stylar end of the ovule but, because of the curvature of that organ, is directed toward the placenta. Similarly the chalazal region faces the placental surface of the ovary (fig. 1).

On the convex dorsal surface, the outer integument is composed of five layers of cells. In younger ovules, it may be seen that the inner four layers have been derived by periclinal divisions from two original inner layers. This integument widens to 7–8 layers (by periclinal division in the two innermost layers, O_4 and O_5, and in the second layer, O_2, from the outer surface) on the lateral faces of the ovule. Ventrally, the outer integument cannot be distinguished easily from the funicular tissues (fig. 2). In this region, the bulk of integumentary tissue is provided by derivatives of the middle layer, O_3, of the five layers continuous from the dorsal side. The four inner strata which have been formed from O_4 and O_5 on the lateral surfaces continue uninterruptedly about the inner integument. The two strata derived from O_2 and the single outer epidermal layer continue as such along the lateral surfaces to the abrupt constriction which marks the funiculus (fig. 2). Aside from this morphological distinction and a somewhat deeper stainability of cells in the boundary region, no indication exists of the sharp anatomical difference which develops later between funiculus and integument.

At the micropyle, this integument terminates in a broad rim (fig. 1), whose cells are placed in a fan-like radiation. The fan-like cell arrangement (*cf.* Sachs', 1878, "coaxial system" or "Springbrunnen" cell arrangement) is more pronounced at the ventral region of the micropylar rim (fig. 3), which is almost in contact with the placenta. Although some periclinal divisions may be seen in various layers of the outer integument (very much predominating at the rim), most divisions at this stage are anticlinal. In the outer epidermal layer, O_1, the cells are radially elongated to a slight extent, particularly at the anterior micropylar rim (fig. 3).

A single vascular bundle enters the ovule from the posterior region of the funiculus (figs. 1 and 15). In the outer integument, this bundle branches in three, with one branch passing to the base of the nucellus and the other two recurving through the ventral region of the outer integument, on each

side of the median plane of the ovule, toward the anterior end (fig. 2). Some tracheary and sieve elements may be found in the single chalazal bundle; but the other two bundles are still procambial, and their cells are distinct principally by their elongated shape and deeper stainability.

An inner integument lies within the outer one. It is free from the latter and from the nucellus down to the base of the nucellus (fig. 1). This integument consists of two distinctive strata (fig. 3): an inner single-celled layer of larger and more or less isodiametric cells in which anticlinal divisions predominate; and an outer layer, one to four cells wide, in which the cells are smaller, less densely stained, and more or less tangentially elongated. Pericinal divisions occur randomly throughout the outer of the two layers to produce the variations in thickness noted above; otherwise, cell divisions in this layer are mainly anticlinal. At the micropyle, the inner integument broadens to form a knob-like rim, about 3–4 cells thick, which is completely contained within the outer integument. The opening through this rim is rather large and is occupied by the tip of the protruding embryo sac, covered by a thin layer of disintegrating nucellar tissue.

Development of the seed coat (testa). Two days. Fertilization occurs within a day or two after the flowers have opened and is attended by immediate growth activity in the two integuments. The first sign of growth appears at the dorsal ridge of the seed in the innermost two layers of the outer integument. In the inner epidermis of this integument, O_5, divisions in various planes produce two to three layers of cells. Simultaneously, cells of the adjacent layer, O_4, divide periclinally and anticlinally to form two to three layers. Layer O_2 also gives rise to two layers of cells here. In this manner the dorsal ridge of the outer integument soon acquires a similar construction to the lateral regions. The other layers of cells, O_1 and O_3, of the outer integument divide anticlinally only during these first two days, and radial elongation in O_1 becomes more marked (fig. 4). In the integument rim, the "Springbrunnen" activity continues to produce longer series of fan-like cell rows, particularly at the anterior region, and becomes less pronounced in the ventral portion of the rim. Anticlinal divisions proceed in both strata of the inner integument, and more periclinal divisions may occur in its outer stratum.

Four days. After 3–4 days, the innermost region of the outer integument, derived from O_4 and O_5, is composed of 6–8 layers of cells; the third layer, O_3, is 2–4 cells thick and procambial strands differentiate in it; the next layer, O_2, is divided into two to three layers of cells; and the outer epidermis remains uniseriate. The cells of the outer epidermis, which rarely divide periclinally, are destined to become the characteristic rod-shaped Malpighian or palisade cells. At this time, marked radial elongation of these cells occurs in the anterior portion of the micropylar rim (fig. 5) and

along the ventral flanks of the integument adjacent to the funiculus (fig. 15). In a transverse section of the young seed, the elongation of these integumentary cells serves definitely to mark the boundary between integument and funiculus, a distinction which is further emphasized by the occurrence of periclinal walls in the epidermal cells of the funiculus and the formation of an arillate protrusion from the dorsal side of the funiculus (figs. 6 and 15, at arrow). Periclinal divisions in the median plane of the seed mark the initial blocking out of the future "tracheid island" (fig. 6). In the micropylar area, the intensive periclinal and anticlinal activity of the "Springbrunnen" meristem continues, producing a large mass of cells in very regular arrangement (fig. 5). The cells of the inner stratum of the inner integument (which is uniseriate throughout its development) elongate radially to about twice the radial diameter of the cells of the outer stratum of that member. In the outer stratum, periclinal divisions may produce a thick band of tissue (fig. 15) on the ventral side of the embryo sac.

Six days. Within the next two days, as seed enlargement progresses rapidly, the border between funiculus and outer integument becomes marked internally by the gradual loss of stainability in the cytoplasm of most of the cells on either side, *i.e.*, ventrally and dorsally. In this way a separation zone 3–4 cells thick, the cells smaller and more deeply stained than their neighbors, serves to delimit the boundary. As yet, these cells have no other distinctive characteristics. The dorsally adjacent cells in the thick portion of the ventral region of the integument (continuous with layer O_3 and now partially layer O_4) continue to divide in the frontal plane to increase the radial extent of this region. Along the lateral and dorsal sides of the ovule, the cells of the innermost 3–5 layers of the outer integument elongate tangentially in the transverse plane. Shortly afterwards, however, they become isodiametric by anticlinal and oblique divisions. Simultaneously, the cells of the outer stratum of the inner integument become isodiametric because of an increased rate of anticlinal divisions.

Less than a week after full bloom, cotyledon formation begins in the rapidly growing embryo. Radial elongation proceeds in the cells of the internal layer of the inner integument to the extent that they acquire a radial diameter 3–4 times that of the cells in the outer stratum. In the outer integument, surface extension is attended by tangential elongation in cells derived from the hypodermal and sub-hypodermal layers (*i.e.*, derived from O_2) and anticlinal divisions in other cells. In the outer epidermis, radial elongation of the cells occurs at different rates in different regions. Thus, at this time, they are 45 μ high in the anterior region of the micropylar rim, 32 μ high on the strophiolar margin adjoining the funiculus (*i.e.*, between

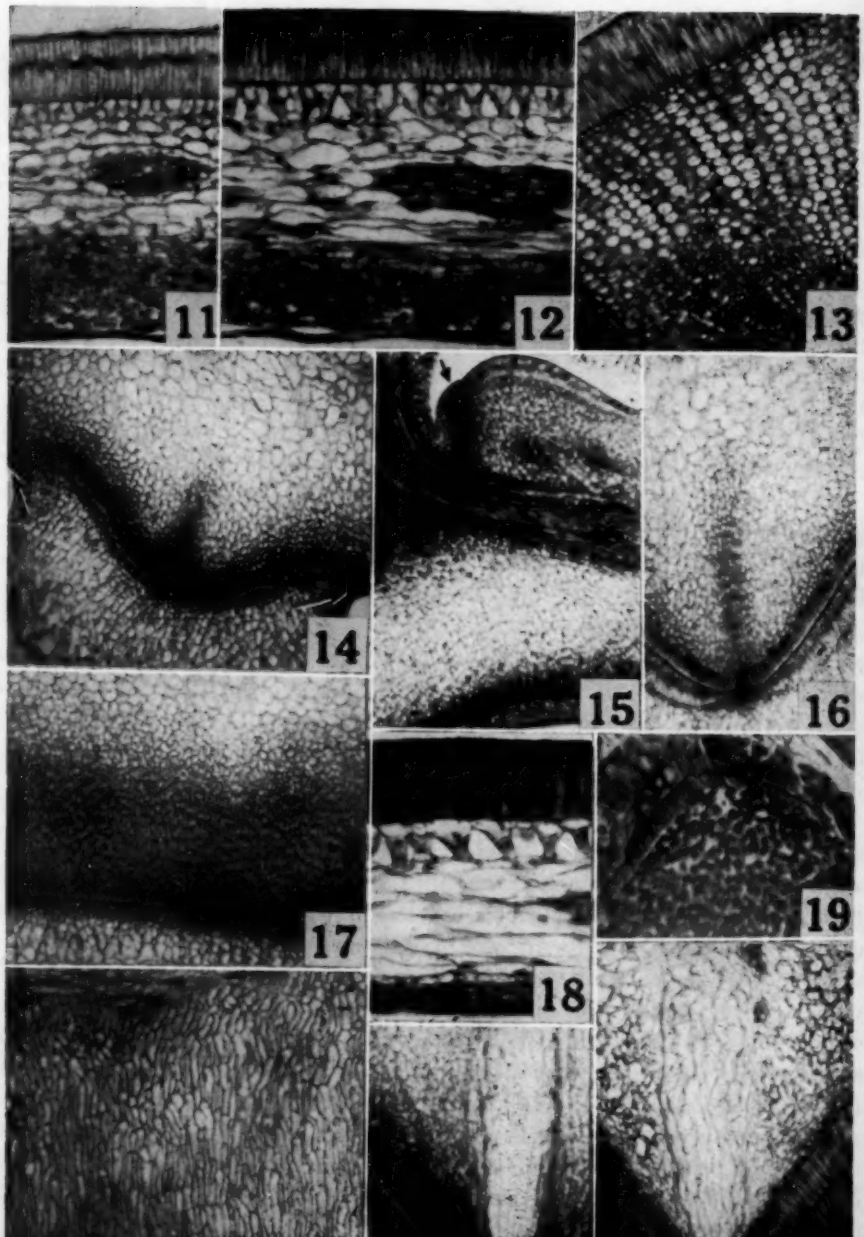
the chalaza and the funiculus), 35 μ in the circumhilar region (at the boundary between funiculus and integument), and grading down to 10 μ (virtually no elongation) on the dorsal surface of the seed. It may be remarked that these size differences of the epidermal cells are maintained relatively during further development of the seed coat.

Eight days. At eight days, zones of differentiation became blocked out in the outer integument. Cells throughout this integument enlarge, and incipient tangential elongation becomes marked in the derivatives of the middle, O_3, and the next outer, O_2, layers. The vascular bundles, many of which are still procambial, branch and re-branch into the lateral flanks of the seed in the region of the derivatives of O_3. In the other layers (12–14 cell strata) of the integument, mitotic activity continues particularly in the form of the anticlinal divisions. About four layers have been produced from O_5, four from O_4, three to four from O_3, two to three from O_2, and O_1 remains uniseriate.

Between funiculus and integument, the boundary or separation region is marked first by radial elongation of a single layer of cells on the integumentary side, closely followed by the elongation of cells in a similar adjoining layer on the funicular side. Dorsally to this double line of elongating cells (*i.e.*, on the integumentary side), a narrow zone is formed in the median plane of the ovule along the length of the hilar region. This zone, which will become the tracheid island, is characterized by the elongation of its cells in the median plane, towards the dorsal surface. While neighboring cells enlarge isodiametrically, the cells of this zone divide actively in the frontal plane and remain deeply staining.

Ten days. By ten days, signs of cellular collapse appear in the outer stratum of the inner integument. The cells of this outer layer are much smaller radially and extended tangentially, but the cells of the inner stratum remain large and become more or less isodiametric as tangential expansion occurs in the seed coat. In the outer integument, the innermost 9–10 layers of cells continue dividing periclinally and obliquely. The other cells of this integument are enlarging and acquiring larger vacuoles. The palisade-like cells of the outer epidermis continue their radial elongation over the whole seed surface, including the dorsal region now, and reach their greatest length of 85 μ in the anterior rim of the micropyle (fig. 8). A cuticle is clearly visible over the surface of the palisade cells at this time. In the tracheid island zone, more and more cells elongate, so that the radial extent of this zone becomes considerably greater. Mitotic activity has ceased completely in the anterior micropylar rim.

Thirteen days. Within three more days, the outer stratum of the inner integument virtually disappears, being represented by a thin structureless membrane. Over the palisade cells of the outer epidermis of the outer in-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tegument, the cuticle thickens markedly. The palisade cells continue to elongate, becoming as much as 130 μ long at the anterior rim of the micropyle (fig. 13) while in the separation layer between funiculus and integument some of these elongating cells are cut in two by periclinal walls. Immediately subjacent to the palisade cells, sporadic periclinal and frequent anticlinal divisions occur in the hypodermal layer. On the lower lateral flanks, air spaces begin to appear in the innermost 10-layered zone derived from layers O_4 and O_5. Air spaces also become noticeable among the cells derived from the "Springbrunnen" activity in the anterior micropylar rim (fig. 13). In the tracheid island zone (fig. 14), divisions in all directions begin to take place concurrently with the cell elongation, but they are predominantly in the transverse plane (fig. 17).

In the larger seeds harvested at this time, the cells of the double separation layer are definitely equivalent to other palisade cells, reaching lengths of 30 μ to 60 μ (fig. 16). Elsewhere, the heavily cuticularized palisade may attain a length of 140 μ (the maximum reached during development) at the anterior micropylar rim; it is up to 70 μ high at the strophiole, and grades down to 20 μ high on the dorsal surface of the seed. Hemicellulosic wall thickenings begin to appear in the palisade cells at the micropylar rim, being initiated along the radial and outer tangential walls. Also in the micropylar rim of larger seeds, there now occurs a radial elongation of the cells of the subepidermal layer, the future "column" cells. In some of the

FIGS. 11–22. All sections are from Henderson Bush seeds. FIG. 11. Median section of dorsal area of seed coat at 31 days. Air spaces beginning to appear in inner zone below and among column cells above. Cuticle development beginning over enlarged palisade cells. Layer of cells adjoining at bottom is endosperm tissue. × 149. FIG. 12. Large seed at 27 days in median section of dorsal area. Note thinning of inner zone, tangential extent of cells in parenchymatous middle zone, funnel shape and large air spaces of column cells, start of wall thickening in palisade cells. × 149. FIG. 13. Anterior micropylar rim in median section at 13 days. Column cells still undifferentiated. × 149. FIG. 14. Transverse section of separation region at 13 days. Arillate rim of funiculus prominent at arrows. Elongation of palisade cells on either side of boundary becoming pronounced. × 92. FIG. 15. Median section of strophiole area at 3 days. Placenta at top of page. Divisions in transverse plane give storied appearance to integumentary cells between inner integument and separation region. Multicellular outer stratum of inner integument conspicuous at bottom. Arrow indicates rim aril. × 92. FIG. 16. Transverse section of separation area at 13 days. Note cell elongation in tracheid island region. × 92. FIG. 17. Median section through tracheid island showing storied arrangement produced by cell divisions in transverse plane. × 92. FIG. 18. Median section of matured seed coat at dorsal region at 41 days. Compression of cells of inner zone and tangential extension of cells in middle zone. × 213. FIG. 19. Median section of extended tip of rim of radicle pocket at 22 days. Above tip is outer stratum of inner integument surmounted by endosperm cells. × 149. FIG. 20. Median section of tracheid island at 45 days. × 92. FIG. 21. Transverse section at hilum at 22 days. Lignification has begun at lower end of tracheid island. Note compact tissue about tracheid island. × 92. FIG. 22. Transverse section at hilum at 41 days. Funicular tissue has been lost during preparation. Note difference in shape of cells of tracheid island below and above. Cells surrounding this region are of stellate type with large intercellular spaces. × 92.

longer, more ventral cells of the tracheid island, (adjoining the separation layer) secondary wall thickenings begin to appear in a reticulate pattern, while the middle lamella becomes lignified. The cells of the tracheid island are usually about 70 μ to 80 μ long at the start of wall thickening. (In smaller seeds at this date, these cells may be only 20 μ to 50 μ long.)

At the strophiole (fig. 9), elongation of the periclinally produced subsurface cells begins to raise the characteristic protuberance. In some of the larger seeds at thirteen days, the cotyledons virtually fill the cavity of the embryo sac. From this time on, it is conceivable that some of the growth of the seed coat is due to passive extension rather than to active elongation on the part of the integumentary cells. Although mitotic activity ceases in most of the cells of the hilar region by this stage of development, it is still being carried on, even in the young palisade cells, along the lateral surfaces of the outer integument and its dorsal ridge.

Fifteen days. At 15 days after flowering, the remaining (inner) stratum of the inner integument begins to disintegrate, and its cells collapse radially. In the separation layer, the palisade cells cease elongating. They range in size from 0 μ (*i.e.*, absent, in the hilar groove along the median plane of the seed) to about 100 μ, depending on their position in the layer. Soon thereafter, wall thickening begins in these cells. Although the nucleus of the cell is located at the dorsal end of the integumentary palisade cells of the double separation layer, it is found at the ventral end of the funicular palisade cells. Later, the incidence of wall thickening leaves a widened lumen at the dorsal end of the integumentary palisade cells, but in the funicular palisade cells, the widened lumen occurs at the ventral end. At the strophiole, elongation of the subepidermal cells forms a long arcuate pattern about seven cells deep. No intercellular spaces occur here during this elongation. At the anterior micropylar rim and at the chalaza, the subepidermal column cells continue to elongate. However, their length does not approach that of the subepidermal cells at the strophiole.

The radicle "pocket" in the seed coat becomes more conspicuous at this time. It will be recalled that the embryo sac and nucellus are curved in the median plane at the time of fertilization (fig. 1). After fertilization, as the cells of the outer integument divide, those cells lying ventrally to the gametophyte cavity (fig. 7) divide more actively by radial divisions than those in the region adjoining the separation layer (fig. 15). As a consequence, a mass of tissue in the form of an extended lip is produced dorsally to the young embryo at the micropylar end of the gametophyte, and the embryo is constrained to bend sharply in its growth to accommodate to the angular turn thus created. Growth in the extended lip of integumentary tissue continues by mitotic activity followed by cell elongation. This lip becomes extremely long during further seed enlargement, ultimately de-

veloping large intracellular spaces among the elongated cells (fig. 21).

Twenty-two days. One week later (at 20–22 days), the last remnants of the inner integument become thinner and begin to be resorbed (fig. 10). On the flanks of the seed, the cells of the 14–15 inner layers of the outer integument (derived from O_4 and O_5) become greatly extended in the tangential direction and much shortened radially. Intercellular spaces of notable size arise among these cells, which appear mycoidal in tangential view (as noted by Haberlandt 1877, and Pammel 1899). In the next adjoining zone lie tangentially elongated cells of much larger radial diameter, without noticeable arms or perceptible intercellular air spaces. As mentioned above, vascular bundles occur among the cells of this tissue. In these parenchymatous cells and in the column cells occur numerous starch grains of both simple and compound structure. These starch grains increase in size and number up to about 30–31 days. At the dorsal ridge of larger seeds at this time, the unthickened palisade cells may reach the limit of their elongation (55 μ to 60 μ high), and some air spaces begin to appear among the mycoidal derivatives of O_4 and O_5. This development occurs by the 31st day in seeds of normal size (fig. 11).

The general trend in differentiation in the various regions of the outer integument (anterior micropylar rim first, then the hilar rim and strophiole, chalaza, flanks of the seed, and finally the dorsal ridge) appears to occur with each of the different tissues of that integument. At 20 days, the cells of the column layer on the flanks of the seed are elongating while those at the dorsal ridge are unelongated or just starting to elongate (fig. 10). It may be seen that two or three of the column cells abut on one underlying cell, indicating that usually one to two subsequent anticlinal divisions followed the original periclinal division creating the layer of column cells and the underlying layer. At the micropylar, circumhilar, and chalazal regions, the osteoform cells of the column layer are separated by air spaces, being in contact mainly by projections from each end of the cell. However, many of these cells also have other lateral protrusions in contact with similar processes from their neighbors. The diameter of these cells is much greater at the end adjoining the palisade layer than at the opposite end, so that a funnel shape often obtains. Not infrequently the cells are divided in two by periclinal walls.

At the hilum, the cells of the tracheid island have ceased elongating (fig. 21). These cells are about 75 μ long at the separation layer but become shorter and contorted deeper (dorsally) in the integument, as though their radial growth had been restricted. The whole tracheid island zone is about 650 μ high, 100 μ wide, and 5000 μ long. It traverses the length of the center of the hilum, in the median plane, along the hilar groove up to the vascular bundle which supplies the seed. Lignification of the secondary wall becomes

conspicuous (with the phloroglucinol-HCl test), developing first in cells adjacent to the separation layer and then proceeding dorsally, as mentioned also by Pfaefflin (1897).

About the rim of the hilum, the elongate funicular cells ventral to the palisade cells of the separataion layer acquire wall thickenings and block out a more or less distinct saucer-like aril (Pfeiffer 1891) or "rim aril" (Corner 1951). No intercellular spaces occur among these cells. In later development, particularly at seed ripeness, this rim aril adheres tightly to the seed coat but can be removed cleanly after the seed is soaked. Dorsal to the separation layer, the walls of the non-columnar subepidermal cells become thicker. These thickened cells occur 2–3 layers deep throughout the hilum region. The other cells here, which make up the bulk of the ventral region of the inner integument, are thin-walled, parenchymatous cells, with small intercellular spaces at their interstices. Subsequent seed enlargement brings about a great enlargement of these intercellular spaces and a stellate shape to the parenchymatous cells.

Thirty days. As growth continues, each phase of differentiation spreads out in a wave from the initiation center at the anterior micropylar rim of the outer integument through the pattern noted above. The development of wall thickenings in the palisade cells and of air spaces between the column cells follows this course (fig. 12). In the palisade cells, the "light line" appears just below the cuticle. It is especially noticeable in the cells of the integumentary portion of the separation layer, where a second, broader light line, which is particularly evident with polarized light, appears half-way along the length of the cell (fig. 22). No noticeable light line occurs in the funicular palisade cells, which fact was also noted by Pfaefflin (1897). In the subepidermal cells of the hilar region, wall thickenings increase in size, and the zone of thickened cells extends farther inward in the integument (to 5–6 cells in depth) and also begins to embrace cells in the region of the micropyle. In those cells immediately adjoining the palisade layer of the hilum, trabeculae (rod-like wall thickenings which traverse the cell lumen) begin to appear. At the strophiole, the rows of subsurface elongated cells, which serve to raise this eminence on the seed coat, remain without intercellular spaces. They begin to acquire thickened walls within 30 days after flowering.

Thirty-four days. When optimum edible maturity is reached, about the 34th day, the palisade cells over the entire seed are starting to develop extensive wall thickenings, which are characteristically fluted at their outer ends. The cells of the column layer at the adaxial micropylar rim are also acquiring wall thickenings. In the tracheid island, lignified secondary walls are being thickened in a pitted-reticulate pattern, with slight over-

arching borders at the pit rims. (Thickened walls elsewhere are composed principally of hemicellulose, as indicated by hot orcinol-$FeCl_3$-HCl, Reeve 1946a.) The only lignified tissues in the nature seed coat are tracheid island cells (figs. 20 and 22) and the tracheary elements of the vascular bundles. In addition, lignification appears at this time in the middle lamella between the two layers of palisade cells making up the separation layer of the hilum. The cells surrounding the dorsal part of the tracheid island remain thin-walled and are separated from each other by large intercellular spaces. Contact between these stellate cells is maintained only by their extended arms. In median and transverse sections, the large cells of the layer enclosing the vascular bundles are up to 130 μ long tangentially on the flanks of the seed (fig. 18).

The innermost layers of the integument (mycoidal parenchyma) seem much compressed, and the narrow cells lie very close together. Because of the great amount of tangential extension of the seed coat, this region now is composed of only 7–8 layers of cells, accommodation to this growth apparently having been accomplished by cellular displacement. Starch grains can no longer be found in the seed coat. No remnants of the inner integument are preserved at this time save at the rim of the extended integumentary lip at the radicle pocket. In this lip, the interior cells of the outer integument are greatly elongated, have extended arms, and are separated by large intercellular spaces (fig. 19). They show no signs of the compression characteristic of the interior integumentary cells elsewhere.

Forty-five days. Up to the 45th day, the program of wall thickening proceeds further in the cells of the palisade layer and in the underlying layer of column cells on the flanks and dorsal ridge of the seed coat (fig. 18). The enlarging embryo compresses and distends the tissues of the seed coat slightly more. Following this date, the seeds begin to dry out and shrink. This latter program was not studied in the present investigation.

Discussion. The uniformity of construction of the mature seed coat of members of the Leguminosae has long been noted by many botanists. Deviations in details of seed coat structure are also characteristic and have served to permit generic and even specific descriptions (Mattirolo & Buscalioni 1892, Pammel 1899, Harz 1885b, Winton & Winton 1935, etc.). Similarly, the structure of the immature ovule is exceedingly uniform throughout the family: usually there exists a more massive outer integument, which encloses a thin 2-layered inner integument, inside which is a nucellus whose apex is often disintegrated by a protruding embryo sac (Hofmeister 1858, Brandza 1891, Coe and Martin 1920, Pitot 1935b, Fedorchuk 1944, Corner 1951, etc.). Here again slight deviations in this construction are often of taxonomic significance, *vide* the single integument of the ovule of *Lupinus* (Schleiden & Vogel 1839, Hofmeister 1858), the diametrically opposed uni-

lateral development of the two integuments in *Medicago* (Farley and Hutchinson 1941) etc.

Also common among most Papilionatae is the course of vascularization in the seed coat. Contrary to the implication of Rau (1950), an extensive vascular supply is characteristic of the outer integument of many legumes. Van Tieghem (1872), LeMonnier (1872), and Mattirolo & Buscalioni (1892) have described some of the variations in vascularization which may occur in different genera of this family. As is the case in *P. lunatus,* in many papilionates the ovular bundle passes to the chalaza and gives off two branches in the ventral portion of the outer integument, which then pass around the hilar area toward the anterior end of the seed.

The morphological nature of the so-called "tracheid island," which is also a characteristic manifestation of the papilionate seed, is not clear from the present developmental study. Its physical continuity with the facing xylem of the ovular bundle suggests a tracheary origin and a resemblance to the transfusion tissue so common in coniferous leaves. Unlike the sclerenchyma (palisade and column cells) of the seed coat, but like the tracheary elements of the vascular bundle, the cells of the tracheid island are lignified. Whether the two recurving vascular bundles on either side of the median plane of the young seed play any role in the initial differentiation of the tracheid island in that median plane is unanswered.

Lignification also occurs elsewhere in the seed coat of the lima bean. Previously Mattirolo and Buscalioni (1889) reported that only *Baptisia* contains lignin outside the tracheid island and the vascular bundles: in the form of granular deposits in the cuticle. However, the present study shows lignin formed in the boundary substance between the two rows of palisade cells at the hilum of the lima bean. [An interesting relation to maturity determination lies in the first formation of noticeable lignin (by phloroglucinol-HCl test) at the time of optimum edible maturity, following which the lignin stain becomes considerably darker as the seed ages.] Harz (1885a) described lignification of a few parenchymatous cells at the hilum of some leguminous species (especially *Lupinus*), but this does not appear to occur in *P. lunatus.* The hemicellulosic nature of other wall thickenings, as found by Castoro (1906), Schulze and Godet (1909), and Reeve (1946a) was confirmed in this study. The formation of trabeculae, rod-like wall thickenings which traverse the cell lumen, has been recorded for the hypodermal cells at the hilum by Mattirolo and Buscalioni (1892).

In the development of the seed coat, little attention has been directed to changes occurring in the inner integument. The periclinal activity noted in its outer stratum may likewise occur in other species. For example, in the garden pea, Yocum (1922) describes the inner integument as being composed of 6–8 rows of cells. In *P. vulgaris,* Brandza (1891) notes that division probably occurs in the outer stratum to form occasional cells be-

tween inner and outer strata, but this is not mentioned by Haberlandt (1877). Although Pammel (1899) finds 1–4 layers of cells in the inner integument of members of the Caesalpinieae, he states that in the Papilionaceae there is usually a single row of cells. Occasionally three layers are found in the inner integument of *Trifolium,* according to Martin (1914).

During the present investigation, it has been noted that differentiation occurs first at the anterior rim of the micropyle, and that the cells in this region are larger than elsewhere in the seed coat. Haberlandt (1877) also found the largest palisade cells in this region in the common bean. However, in other members of the Leguminosae, the greatest development appears to occur elsewhere. In *Ervum* and *Vicia,* for example, Beck (1878) found the largest palisade cells at the chalaza. In *Pisum,* according to Reeve (1946b), they occur at the strophiole. Schleiden and Vogel (1839) reported them at the chalaza of *Lupinus.* Among several genera with characteristically "hard-shelled" seeds (*Medicago, Melilotus, Trifolium, Trigonella,* and *Astragalus*), Zimmermann (1936) noted the longest palisade cells at the strophiole.

The disappearance of starch from the parenchymatous cells and from the column cells of the outer integument seems to be correlated with the accelerated development of wall thickenings in palisade cells along the lateral flanks and dorsal ridge of the seed. Netolitzky (1926) believes that the two phenomena are causally related. It is of practical interest to note that these events take place at about the time the seed is at the optimum edible quality. The later sequences of maturation lead to a greater thickening of the cell walls in both the palisade and column layers and a consequent increase in toughness of the seed coat. No instances of encapsulation of starch grains in the integumentary cells, as found for example by Buscalioni (1896) in *Vicia* and Tangl (1878) in *Pisum,* occur in the lima bean.

SUMMARY

1. A developmental study of the seed coat of the lima bean was undertaken in conjunction with other studies directed toward the determination of relative maturity of beans used for freezing.

2. The inner integument of the ovule is composed of two strata: an inner single layer of cells and an outer stratum which varies from one to four cells thick at places, according to the number of periclinal divisions which have occurred. Both strata of this integument disappear in centripetal order during seed coat ontogeny.

3. The outer integument is composed initially of five strata of cells.

4. The innermost two give rise to fifteen layers of cells which elongate and produce long arms in the form of "mycoidal parenchyma," becoming much compressed at seed ripeness.

5. The middle and next outer strata produce several layers of cells, of which all but the outermost become large, tangentially elongated parenchyma. The vascular bundles are embedded in this parenchyma. This group of cells also constitutes the bulk of integumentary tissue at the hilum. In the outermost of these layers, *i.e.* the subepidermal layer, are formed the characteristic column cells, separated by large lacunae.

6. The outer epidermis remains uniseriate, and its long narrow cells become the palisade layer.

7. Initial development of the palisade and its largest cells occur at the anterior micropylar rim, which is raised early by meristematic activity of the coaxial type.

8. At the hilum, development of the tracheid island and the double separation layer occurs as in other papilionate seeds.

9. A rim aril is formed from the adjoining thick-walled cells of the funiculus.

10. Correlated with optimum edible maturity of the seed are the following phenomena: disappearance of starch from the parenchyma cells of the outer integument; development of hemicellulosic wall thickenings in palisade cells over the entire extent of the seed coat; and formation of lignin in the middle lamella between the two adjoining palisade layers at the hilum.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 81, NO. 4, PP. 288–299 JULY, 1954

THE STRUCTURE AND DEVELOPMENT OF THE CARYOPSIS IN SOME INDIAN MILLETS. III. PASPALUM SCROBICULATUM L.

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The bibliographic considerations required in the study of grass embryology have been abundant during the past quarter of a century since an extensive literature exists both with regard to the formation of the female gametophyte and to the embryology. A study of the embryology of some cultivated Indian millets, however, was attempted in order to elucidate the post-fertilization history i.e., the transformation of the pistil into the caryopsis in this comparatively little known group of plants. *Paspalum scrobiculatum*, commonly known as the Koda millet, was one chosen for investigation from among others such as *Setaria italica*, *Pennisetum typhoideum*, *Echinochloa frumentacea* and other members of the tribe Paniceae.

The earliest reference to the genus *Paspalum* is contained in the classical work of Kennedy (1900) who has described the structure of the embryo of *P. pubiflorum glabrum*. Shadowsky (1926) and Bennett (1944) have published accounts of the embryology of the pasture plant *P. dilatatum*. In tracing the developmental history of the embryo Bennett paid particular attention to the rate and sequence of growth of its various parts. The present paper deals with the embryology of *P. scrobiculatum* in all its aspects with special emphasis on the structural features of the endosperm.

Material and methods. The plants were grown at the University Botanical Garden from seeds secured from the Millet Specialist, Coimbatore, South India. Young spikelets were fixed in the field in formalin-acetic-alcohol and for post-fertilization stages, the ovaries were dissected out. Dehydration and infiltration were carried out by the customary methods. Sections were cut 12–15 μ thick and stained with either safranin and fast green or with Haidenhain's iron-alum haematoxylin.

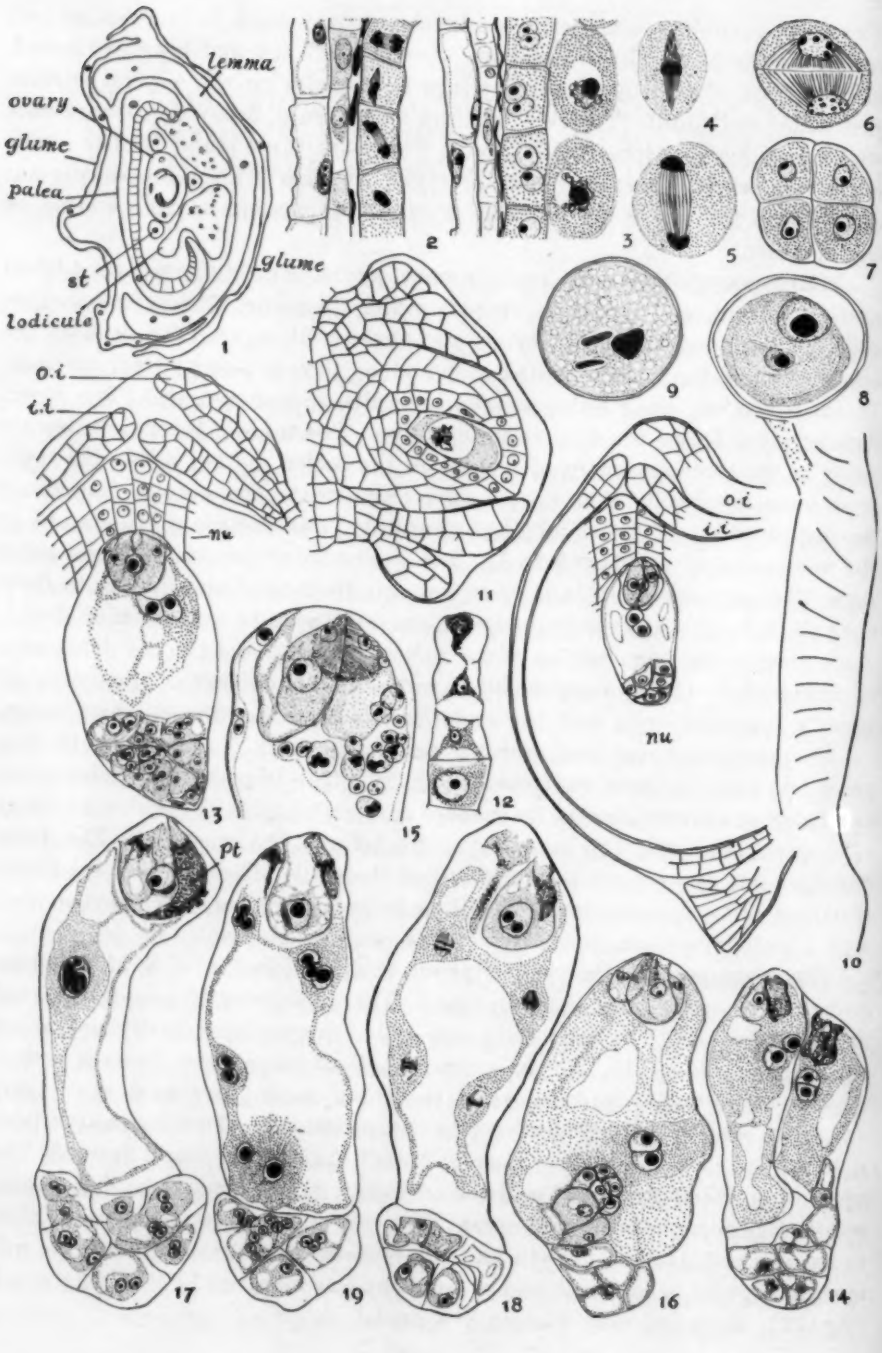
Floral organs. The inflorescence is a panicle consisting of a number of alternating spicate branches of a raceme. The spikelets are 2-ranked and closely imbricate. They are planoconvex, more or less orbicular and borne on a flattened and winged rachis. Each is one-flowered. In all, there are two glumes, a lemma and a palea, the lower empty glume being absent. The first glume is concave, obovate, membranous and 5–7 nerved. The second glume is almost flat and 5-nerved with two prominent submarginal nerves. The third glume is the lemma of the flower. It is more or less orbicular or subovate, coriaceous, brownish in color 5-nerved and minutely striolate.

The palea is similar in structure and color to the lemma. It is bi-keeled and convex at the back. The margins are strongly inflexed and bear two broad, membranous, almost overlapping wings or auricles on the ventral surface just below the middle. The two lodicules are cuneate, fleshy and emarginate with a number of procambial strands. There are three stamens. The ovary bears two widely diverging slender style branches with plumose stigmas exserted on the top of the spikelet. Figure 1 represents a cross section of the spikelet.

Microsporogenesis and male gametophyte. The anthers are 4-lobed and two-celled, and borne on slender white filaments. The pollen mother cells are bounded by an epidermis and three wall layers. The cells of the epidermis are large, thin-walled and rectangular in longitudinal sections. In cross section, their outer tangential walls appear rounded. The hypodermal layer forms the fibrous endothecium. The middle layer degenerates prior to the commencement of meiosis in the pollen mother cells. The tapetum consists of cells that are at first uninucleate but become binucleate during prophase of Meiosis I (figs. 2 and 3). The meiotic divisions are of the successive type (figs. 4 to 7). The microspores possess a single germ pore. The generative cell is more or less spindle-shaped and divides to form the two male cells at shedding (figs. 8 and 9). The tube nucleus may degenerate prior to the germination of the pollen grain. At the time of dehiscence of the anther, the two persistent layers are the epidermis consisting of greatly enlarged cells and the endothecium showing fibrous thickenings.

Megasporogenesis and embryo sac formation. The ovule is at first erect but later becomes anatropous (fig. 10). The hypodermal archesporial cell functions directly as the megaspore mother cell (fig. 11) without cutting off any parietal cell. The inner integument forms the micropyle. The outer one does not cover more than a third of the ovule. The nucellar epidermis abutting the megaspore mother cell undergoes periclinal divisions so that 4 to 5 wall layers are formed when the ovule is mature.

The megaspore mother cell is about twice as long as wide at prophase and three times as long at metaphase I. The nucleus undergoes the normal meiotic divisions. The four daughter cells (megaspore tetrad) are about equal in size (fig. 12). The functional chalazal megaspore shows a prominent nucleus and cytoplasm while the three micropylar ones are highly vacuolate and ultimately destined to degenerate. By three successive divisions in the surviving cell, a normal 8-nucleate embryo sac is formed. The egg cell is nearly spherical and the two synergids are pear-shaped. A conspicuous filiform apparatus is absent. The two polar nuclei are situated close to the egg cell. During growth and enlargement of the embryo sac, the primary antipodal cells divide and redivide and as many as 15 cells may result (fig. 13). Each cell may contain 1–4 nuclei.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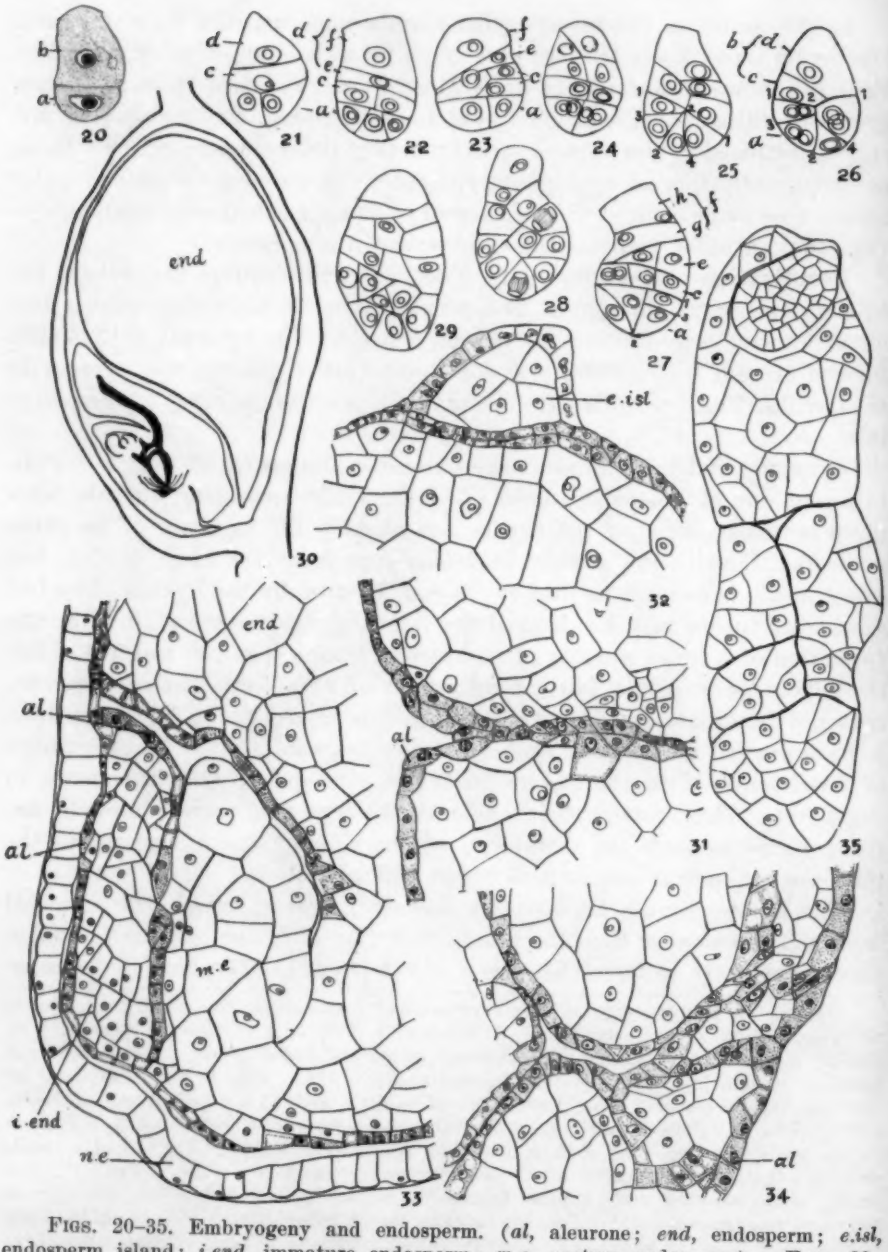
In the course of the investigation certain abnormalities were observed. One ovule showed two embryo sacs lying in close juxta-position (fig. 14). Each sac showed a normal egg apparatus but there seemed to be a common group of antipodal cells, probably due to overlapping. Embryo sacs of several unfertilized ovules showed supernumerary polar nuclei (fig. 15). These are apparently formed by secondary divisions of the original pair of polar nuclei. One ovule showed what appeared to be a six-celled antipodal embryo (fig. 16). In other respects the embryo sac was normal.

Fertilization and embryogeny. The pollen tube enters the embryo sac by penetrating the micropyle. The persistent tip of the pollen tube is frequently seen lying close to the egg on one side. The crescent of X-bodies formed around the egg and also common in other grasses, was present in most ovules. The synergids were disorganised prior to the entry of the pollen tube.

Syngamy and triple fusion take place simultaneously (fig. 17). Fertilization of one of the polar nuclei or of the fused secondary nucleus takes place normally. That of the egg is indicated by the presence of an extra nucleolus. Usually the smaller nucleolus represents the male gamete, but sometimes it is as large as that of the egg. Eventually the nucleoli fuse but sometimes fusion may be delayed for a considerable time until after the formation of a large number of endosperm nuclei (figs. 18 and 19). Thus the zygote undergoes a fairly long period of rest. Fertilization, however, does not terminate the life of the antipodals immediately. They continue to be active till the cellular phase of the endosperm. They act as reservoirs of nutriments. With the expansion of the endosperm, they commence to degenerate. They retain their chalazal position and their remnants are recognisable towards the distal end of the cellular endosperm up to the time the proembryo commences organ differentiation.

The zygote divides transversely into two cells of which the terminal cell *a* may be smaller than the basal cell *b* (fig. 20). The basal cell divides, also transversely to form the cells *c* and *d* (fig. 21). The next division oc-

FIGS. 1–19. Microsporogenesis, embryo sac and fertilization. (*i.i*, inner integument; *nu*, nucellus; *o.i*, outer integument; *st*, stamens). FIG. 1. X.s. through spikelet. ×20. FIG. 2. L.s. portion of anther wall showing epidermis, endothecium, degenerated remnants of middle layer and dividing tapetal nuclei. ×375. FIG. 3. Same, showing binucleate tapetal cells. ×375. FIGS. 4–7. Meiosis I and II in pollen mother cells. ×375. FIG. 8. Pollen grain showing tube and generative cells. ×375. FIG. 9. Pollen grain showing tube nucleus and two sperm cells. ×375. FIG. 10. L.s. ovule showing anatropous, crassinucellate and bitegmic condition. ×196. FIG. 11. L.s. young ovule showing hypodermal megaspore mother cell. ×196. FIG. 12. Linear tetrad of megaspores. ×375. FIG. 13. Embryo sac at pollination. ×196. FIG. 14. Twin embryo sacs lying in close juxta-position. ×196. FIG. 15. Upper portion of embryo sac showing egg apparatus and supernumerary polar nuclei. ×196. FIG. 16. Abnormal embryo sac showing formation of antipodal embryo. ×196. FIG. 17. Syngamy and triple fusion. ×196. FIG. 18. Zygote showing two nucleoli indicating fertilization. ×196. FIG. 19. Embryo sac showing zygote and free endosperm nuclei. ×196.



FIGS. 20–35. Embryogeny and endosperm. (*al*, aleurone; *end*, endosperm; *e.isl*, endosperm island; *i.end*, immature endosperm; *m.e.*, mature endosperm). FIGS. 20–29. Developmental stages of embryo. ×200. FIG. 30. L.s. mature caryopsis. ×21. FIG. 31. Involution of aleurone from periphery of endosperm. ×88. FIG. 33. Lobing of distal end of endosperm resulting from involution of aleurone. ×200. FIG. 34. Involution of aleurone in different directions inside mature kernel. ×88. FIG. 35. Lobing of endosperm probably from splitting of middle lamella between cells. ×180.

curs in the terminal cell and is vertical and a 4-celled proembryo is formed. The cell *d* undergoes a transverse division to give rise to the cells *e* and *f*, the latter forming the suspensor initial, while the cell *c* adjacent to the terminal cell divides vertically (fig. 22). One of the two cells of the tier *c* thus formed, next divides transversely (fig. 23). The terminal pair of cells again divides vertically but at right angles to the original wall and forms a quadrant (fig. 24). Occasionally, however, oblique vertical divisions occur in the terminal cell so as to cut off a central apical cell (fig. 22). Figures 25–28 show anomalous division in the terminal tier. 1–1 represents the original cell wall dividing the zygote into two, and 2–2 the cell wall dividing the terminal cell vertically. Further divisions are obliquely vertical as represented by cell walls 3 and 4 in each of the terminal pair of cells. Figure 27 shows a proembryo in which one of the pair of terminal cells has divided transversely as represented by cell wall 3, and the other obliquely as shown by cell plate 1–2. The sequence of further divisions could not be followed with any definiteness as divisions occurred irregularly in all planes (fig. 28). Periclinal divisions in the embryonal mass cut off the dermatogen (fig. 29). The suspensor cell may undergo a few transverse divisions followed by vertical ones but unlike other millets, it is but a short structure. The differentiation of the plumule-radicle axis conforms to that usually described for grasses. The scutellum is inserted on the axis directly below the plumule-sheath (fig. 30). The portion facing the endosperm may bear one or more protuberances and sometimes secondary protuberances numbering as many as seven are present.

Endosperm. The primary endosperm nucleus formed by the fusion of the second male nucleus with the two polar nuclei, or with the secondary nucleus, divides soon after formation. The two nuclei thus formed divide again. Of the 4 nuclei, two remain at the micropylar end of the embryo sac while the other two migrate to the chalazal end. Figures 18 and 19 show the formation of a large number of free endosperm nuclei before syngamy is complete. Twenty-four free nuclei are observed when the proembryo is 2–4 celled. Cell wall formation begins from the periphery towards the centre. The peripheral layer cuts off rows of endosperm cells towards the inside. With the cessation of meristematic activity it forms the aleurone layer. The antipodals retain their position though disorganised. Later, only darkly stained streaks are seen closely adhering to the distal end of the endosperm. With the maturity of the endosperm the cells are filled with starch grains. The nuclei become squeezed and distorted by the crowding together of the starch grains as evident from their irregular outline, weak staining reaction and disappearance of nucleoli.

Certain features of special interest were noted in the course of endosperm development:

1. There are frequent involutions of the aleurone layer from the periphery towards the centre of the endosperm tissue (fig. 31).

2. The involuted aleurone resumes its meristematic activity, cutting off regular radial rows of endosperm cells.

3. In such kernels young endosperm cells of smaller calibre recognisable by their prominent nucleus and cytoplasm, are interspersed among the larger mature endosperm cells which are filled with starch grains.

4. Small islands of starch-filled mature endosperm cells ensheathed by the aleurone are formed towards the distal end of the main body of the endosperm (figs. 32 and 33), as a consequence of involution of the aleurone. Where involution has occurred, the involuted aleurone forms a double layer.

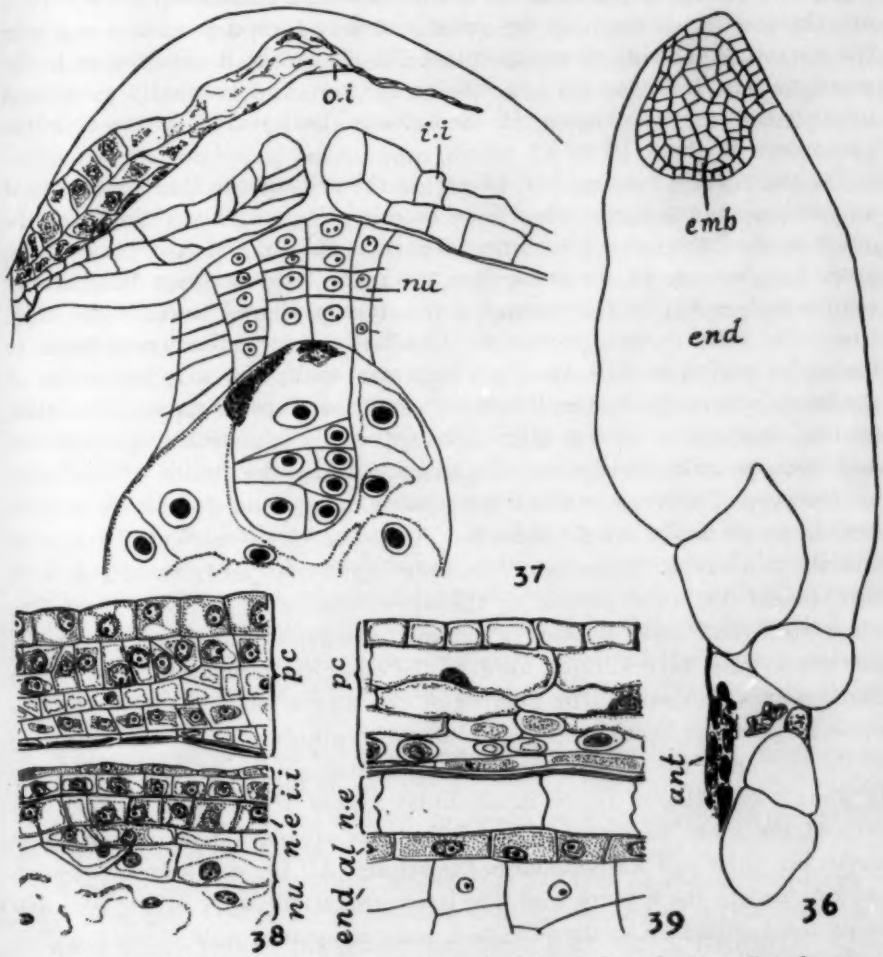
5. Such peripheral involutions of the aleurone may ramify inside the mature endosperm cells (fig. 34). Wherever it is double, it may become separated by a space, thereby resulting in the splitting of the main body of the endosperm into as many lobes as there are involutions. Meristematic activity may be resumed along the regions of involution.

6. The formation of islet meristems is not confined to the distal end of the kernel but may also be formed at the sides depending on the nature of the involution. Figure 33 shows the formation of two lobes or islands towards the distal end of the endosperm, each ensheathed by the aleurone. The exact significance of these structures is discussed elsewhere.

7. In some instances lobing of the endosperm occurs in a different way even before the proembryo commences organ differentiation and before the surface layer of the endosperm begins to function as a resting cambium (figs. 35 and 36). Probably this phenomenon results from splitting of the middle lamella between cell walls instead of by involution. Each separate lobe is not bounded by aleurone. In still others, the main body of the endosperm appears to be split into two equal halves presenting the false appearance of two separate embryo sacs, but serial sections indicate clearly that these regions are contiguous.

Seed and fruit. *Nucellus.* The nucellus consists of parenchymatous cells which vary in shape from rectangular to elongated. At the time of fertilization it is delimited on the outside by a definite layer of cells, the nucellar epidermis. In the region of the micropyle the embryo sac is bounded by 3 to 5 cell layers of the nucellus formed by periclinal divisions of the nucellar epidermis (fig. 37). By the time the cellular phase of the endosperm has begun, the disorganisation of the nucellar cells is already quite advanced. With the endosperm filling the cavity of the embryo sac the collapsed remnants of cell walls and nuclei are observed in the vicinity of a distinct nucellar epidermis (fig. 38). As the endosperm expands the nucellar cells towards the basal end collapse earlier than those towards the stylar end. As the young caryopsis reaches maturity, the endosperm abuts

directly against the persistent nucellar epidermis (fig. 39). Meanwhile the outer tangential walls of the latter appear suberised and the cells become devoid of any cell contents. This layer survives in the caryopsis of even a



FIGS. 36–39. Fruit. (*al*, aleurone; *ant*, antipodals; *emb*, embryo; *end*, endosperm; *i.i*, inner integument; *nu*, nucellus; *n.e*, nucellar epidermis; *o.i*, outer integument; *pc*, pericarp). FIG. 36. Embryo and endosperm with remnants of degenerated antipodals. ×50. FIG. 37. Micropylar portion of ovule showing commencement of disorganization of outer integument. ×130. FIGS. 38, 39. L.s. peripheral portions of mature caryopsis. ×130.

fairly advanced age and constitutes the perisperm. It is, however, possible that certain cells of the layer may disorganise, as evident from their radial walls which remain thin and wavy and in a state of resorption.

Testa. There are two integuments of which the inner is typically two-layered and forms the micropyle. The outer is 3-layered in the integument-insertion region and 5 to 6 layered in the region near the tip, forming a hump and gradually thinning out towards the rim. It does not grow beyond one third of the distance up the ovule, and may form a hood or a cap over the micropyle. During development of the caryopsis, it commences to degenerate, first from the tip (fig. 38) or the rim, and gradually progresses towards the insertion region. It has entirely disappeared by the time the proembryo is about 10 to 12 celled.

In the portion forming the micropyle the cells of the inner integument appear very much larger than those in other regions. The collapse of the outer layer of the inner integument begins at the time of resorption of the outer integument. At the same time the inner layer becomes tangentially compressed except in the region of the micropyle and towards the style where the cells remain prominent. Gradually disorganisation extends to the stylar region as well. In the mature caryopsis, however, resorption of the inner integument is complete except in the micropylar region. The latter portion appears to survive. Here, the cell walls become highly cutinised and there is an accumulation of pigments filling the lumen of the cells.

Pericarp. The ovary wall at the time of embryo sac formation consists of 5 to 6 cell layers on the sides but is thicker in the region of the style and the funiculus. The cells of the outer epidermis are rectangular with their longer diameters parallel to the circumference of the ovary wall. The inner epidermal layer consists of narrow, elongated and tubular cells. Of the hypodermal layers, those towards the outer epidermis are larger than that towards the inside. The number of cell layers remains practically the same in post-fertilization stages as at the beginning. With the maturity of the caryopsis the cells of the pericarp become greatly stretched and are in a state of collapse. Large intercellular spaces are formed between the cells of the inner pericarp. Some of the cells are devoid of cytoplasm or nuclei but their cell walls undergo thickening. All the cell layers, however, are retained in the mature seed, the inner epidermal layer of the pericarp being firmly attached to the suberised outer tangential wall of the nucellar epidermis (fig. 39).

Discussion. It would be worth while to review the embryological features in *Paspalum* in the light of investigations on other members of the Gramineae. The anther tapetum consists of binucleate cells unlike *Pennisetum* (Narayanaswami 1953) and *Panicum miliare* (author's unpublished work) where it remains uninucleate. Microsporogenesis proceeds normally, the meiotic divisions being of the successive type as in *Paspalum mandiocanum* and *P. conjugatum* (Schnarf 1929).

The ovule is anatropous and the inner integument forms the micropyle. But unlike *Pennisetum* (Narayanaswami 1953) where the rim of the integument never reaches the summit of the nucellus or *Setaria* and *Echinochloa* (author's unpublished work) where it is continued over the nucellus to form a narrow endostome, in *Paspalum*, the tip just meets but does not grow beyond the nucellus. Periclinal divisions of the nucellar epidermis result in a deeply crassinucellate condition of the ovule as compared with *Panicum*, *Setaria* or *Echinochloa* where not more than two layers are observed in the region of the micropyle.

The stages leading to the formation of the mature embryo sac conform to the usual grass type. The synergids are disorganised before the entry of the pollen tube unlike *Euchlaena* and *Zea* (Cooper 1937). An antipodal complex of several cells is formed, each cell being coenocytic and of the glandular instead of the spear-heading type reported in *Sorghum vulgare* (Artschwager and McGuire 1949).

Abnormalities like the formation of antipodal embryos, the propensity of the polar nuclei to divide prior to fertilization and twin embryo sacs are peculiar to the plant. Antipodal embryos are rare and have been recorded only in a few plants such as *Allium odorum*, *Ulmus americana*, *Elatostemma sinuatum eusinuatum*, (see Maheshwari 1950). Supernumerary polar nuclei have been reported in *Saccharum officinarum* (Artschwager, Brandes and Starrett 1929), and twin embryo sacs in *Poa* (Tinney 1940), and in *Sorghum vulgare* (Artschwager and McGuire 1949). During embryogeny the order of cell division is not constant in the two-celled proembryo, and in later stages, this completely obscured the growth pattern. This is in accordance with the observation of Bennett (1944) in *Paspalum dilatatum*.

The endosperm is of the nuclear type and its method of development follows the conventional in all the genera of the Paniceae. The surface layer of the endosperm is a resting 'cambium' as observed by Gordon (1922) in wheat, barley and oats.

Many ovules show certain interesting features in the development of the endosperm. One is the occurrence and significance of a triangular lobe of tissue at the base of the endosperm forming an island. Randolph (1936) reports similar structures in the caryopsis of *Zea mays* and interprets them as the persistence of the maternal tissue i.e., the antipodals, as a small mass of abnormal cells filled with starch. According to him they represent a group of proliferated antipodal cells enveloped by the aleurone layer. The resemblance of such structures in the two genera *Zea* and *Paspalum* is remarkable but my investigations have shown that the continued enlargement of the endosperm towards the stylar end of the ovule is not accompanied by any renewed activity of the antipodals. The antipodals were com-

pletely resorbed with the expansion of the endosperm so as to leave no trace of their former existence.

Critical examination of mature kernels shows that the islands occurring as detached masses of cells merely represent lobes or involutions of endosperm tissue. The aleurone layer follows these involutions appearing as an infolded double layer of cells in the region of involution. Frequently localised activity of the aleurone at the crown end may produce a projecting lobe of tissue ensheathed by the aleurone. In such instances the central group of mature endosperm cells of larger calibre appears enveloped by young immature cells of smaller size and free of starch. Renewed activity of the aleurone layer rather than that of the antipodal cells may then account for the formation of such islands of endosperm. The latter may often appear detached from the main body of the endosperm in the region where the aleurone is double.

In several ovules lobed endosperm is noticed at the distal end of the kernel which remains more or less indented. Occasionally even the main body of the endosperm appears to have been split into two or more portions, but serial sections present unmistakable evidence that these regions are contiguous. Involution is not confined to the distal end of the endosperm but may occur at several points from the surface of the kernel. The small strips of involuted aleurone may resume their meristematic activity producing fresh files of young endosperm cells inside the main body of the mature kernel. These are akin to the secondary meristems.

The above observations are in general accord with those of Sass (1946) on the Argentine variety of waxy maize where similar involutions result in distal lobing. Randolph's view that these structures represent proliferated antipodal cells is obviously incorrect.

SUMMARY

1. The spikelets are one-flowered and have 2 glumes, a lemma, and a palea, two lodicules, three stamens and the ovary.

2. Microsporogenesis is normal and of the successive type. The pollen grains are three-celled at shedding.

3. Meiosis in the megaspore mother cell results in a linear tetrad of spores. The embryo sac is of the Polygonum type. An antipodal complex of coenocytic cells is formed. Abnormalities like the formation of an antipodal embryo, supernumerary polar nuclei and twin embryo sacs have been observed.

4. Fertilization and embryogeny have been studied.

5. The endosperm is of the nuclear type. Frequently involutions of the aleurone layer occur at several points on the surface of the endosperm. The involuted aleurone is meristematic. Small islands of starch-filled endosperm

cells ensheathed by aleurone are cut off towards the distal end of the kernel. This accounts for 'lobing' of the endosperm.

6. The protective layers of the mature caryopsis consist of the suberised nucellar epidermis forming the perisperm, the insertion region of the inner integument and the pericarp.

Acknowledgement. It is a pleasure to record my indebtedness to Professor P. Maheshwari for his helpful criticisms in the course of this investigation.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 81, NO. 4, PP. 300–303 JULY, 1954

A NEW DACRYMYCES

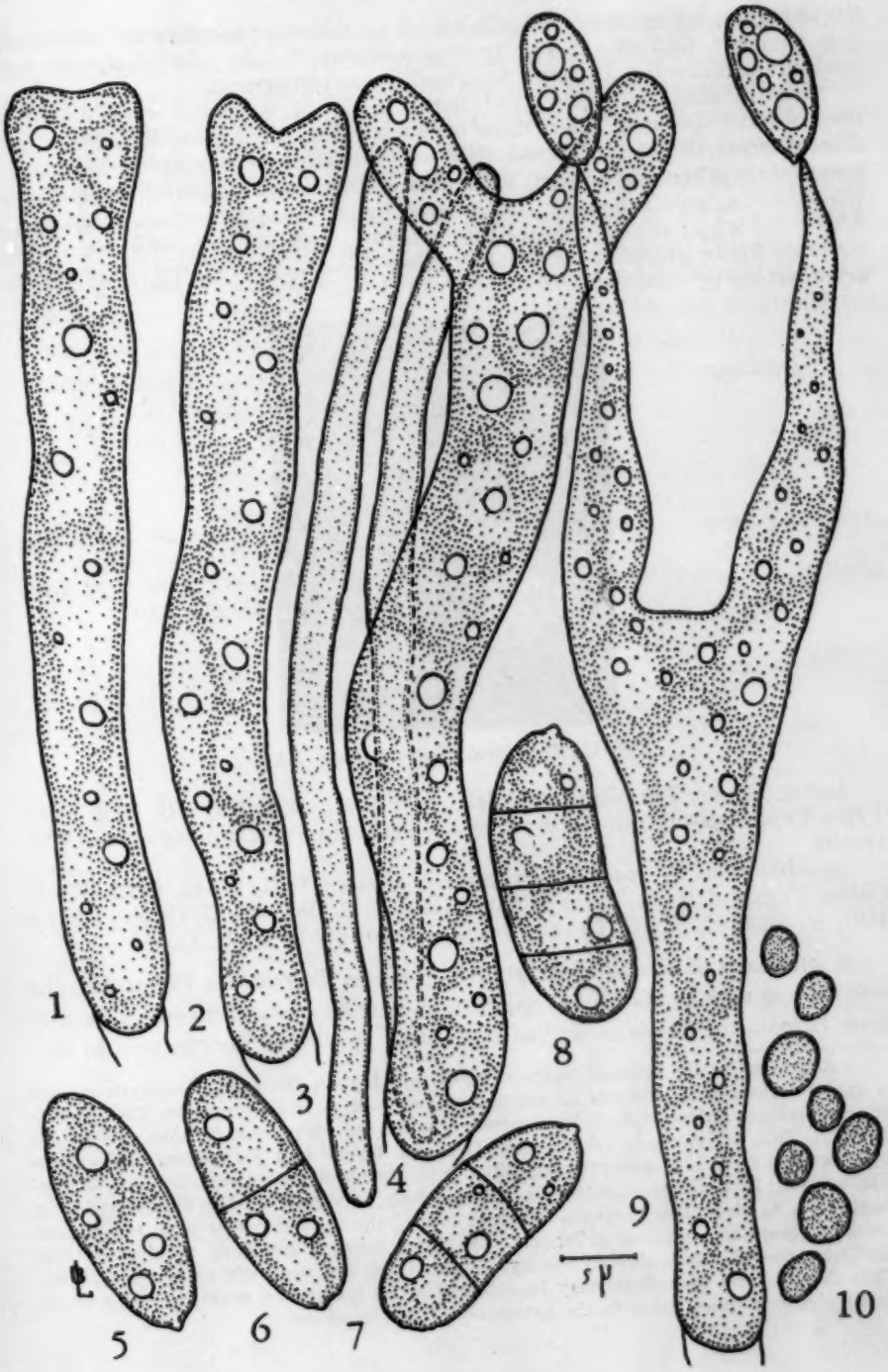
BERNARD LOWY

In the Spring of 1953, while making collections of tremellaceous fungi in the Baton Rouge area, the writer found a *Dacrymyces* which did not appear to conform with any of the published descriptions. It was presently found, however, that Coker's (1920) description of *D. pallidus* bore a certain resemblance to the *Dacrymyces* under investigation. Through the kindness of Miss Goldie-Smith of the University of North Carolina, all of Dr. Coker's original collections, upon which *D. pallidus* was based, were made available for study.

The Dacrymycetaceae constitute a well defined family of the Tremellales, but as Brasfield (1938) observed, "adequate microscopic characters have been lacking in many descriptions of new species." Although color of the fruiting body is not the most significant criterion for the identification of species, with few exceptions, the known species of *Dacrymyces*, during some phase of their growth, develop a red, orange or yellow pigment. It was a variation in this character which led Coker to state that *D. pallidus* "is quite different from any of the other species. It is the palest." Two other species, however, are also partly characterized by the paucity rather than the abundance of their pigments. These are *D. fuscominus* Coker, which Coker (1920) describes as "sordid smoky, with clay tints in places," and *D. minor* Peck, which Brasfield (1938) describes as having a "greenish amber tint when young, becoming dull orange or yellow when older." The new species is easily separated from *D. minor* Peck, not only on the basis of a conspicuous color difference, but in external morphology, size and septation of basidiospores as well as in the nature of the internal hyphae. It also differs markedly from *D. fuscominus* Coker in size of basidia, size and color of mature basidiospores and color of fructification.

Dacrymyces nigrescens sp. nov. (figs. 1–11). Fructificatio gelatinosa, pulvinata, sicca corrugata, primum fusca, postea nigra; basidia matura furcata, (66.5–) 71–86.5 × 6–8 μ; basidiosporae oblongae vel allantoideae, primum aseptata, deinde 3-septata (10.5–) 16–22.5 × (5–) 6.5–8 μ; coni-

FIG. 1. Young probasidium with prominent oil droplets. FIG. 2. Probasidium with epibasidia beginning to form at promixal tip. FIG. 3. Two dikaryoparaphyses with homogeneous granular contents. FIG. 4. Probasidium showing further development of epibasidia. FIG. 5. Aseptate basidiospore, about 24 hours after discharge from basidium. FIG. 6. One-septate maturing basidiospore. FIG. 7. Two-septate basidiospore. FIG. 8. Mature 3-septate basidiospore. FIG. 9. Mature furcate basidium bearing two young basidiospores. FIG. 10. Group of conidia.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dia hyalina, subglobosa, 2.5 × 3–3.5 × 5 μ; dikaryoparaphyseae[1] clavatae, non ramosae, 69.5–86 × 3–4 μ; hyphae nodosae, 2–3.5 μ; basidiosporae per conidia germinantes. In ligno frondoso demortuo crescit.

Fructification gelatinous, pulvinate, becoming wrinkled when dry, 4–5 mm. broad × 3–4 mm. high; dark brown at first, drying black; mature basidia furcate, (66.5–) 71–86.5 × 6–8 μ; basidiospores oblong to allantoid, non-septate when discharged, becoming finally 3-septate, (10.5–) 16–22.5 × (5–) 6.5–8 μ, pale yellow by transmitted light; conidia hyaline, subglobose, 2.5 × 3–3.5 × 5 μ; dikaryoparaphyses[1] clavate, unbranched, 69.5–86 × 3–4 μ, contents finely granular; internal hyphae 2–3.5 μ, with clamp connections; germinating by conidia.

FIG. 11. Fructification in dry state. × 3.5.

Baton Rouge, Louisiana. On dead frondose wood. May 16, 1953. 8251 Type. Type deposited in the mycological herbarium of Louisiana State University.

Specimens of *D. pallidus* examined: Chapel Hill, N. C. 4072, W. C. Coker. (Type of *D. pallidus*); Chapel Hill, N. C. 4967, W. C. Coker; Chapel Hill, N. C. 4752, W. C. Coker; Smith Island. 5001, W. C. Coker.

A summary of the chief differences between *D. pallidus* Coker and the new species may be stated as follows. The new species differs conspicuously from *D. pallidus* Coker as well as from other species of *Dacrymyces* in dry-

[1] According to the common usage of most mycologists, the term paraphysis is used to apply to the sterile elements of Ascomycetes as well as Basidiomycetes. The implication is that no differentiation is required because the structures in both groups are identical. This, of course, is not the case. It is well known that paraphyses in the Ascomycetes arise from a monokaryon mycelium and from a dikaryon mycelium in the Basidiomycetes. In order to clarify this long-standing ambiguity in the application of a single term to structures having a different origin, the following new term is proposed which suggests this critical difference. The term *dikaryoparaphysis* applies to those sterile hyphae of the basidiomycete hymenium which are presently called paraphyses, while the old term paraphysis may be retained in its traditional sense, to apply to the sterile elements which occur in the hymenium of Ascomycetes.

ing black. The original description of *D. pallidus* Coker included no basidial measurements, but the writer, studying the original material, found their average size to be 27.5–36 × 6.5–8 μ. By contrast, mature basidia of the new species measure 71–86.5 × 6–8 μ (fig. 9). Basidiospores of *D. pallidus* Coker are described in the original paper (1920) as "occasionally septate, with one crosswall" and measuring "4–4.5 μ × 10–13 μ," whereas the new species has basidiospores that are finally 3-septate, measuring 6.5–8 × 16–22.5 μ. Basidiospores having more than three septa were not observed, even after the fungus had been in a moist chamber for ten days, at the end of which time 3-septate spores predominated (fig. 8). Conidia are not described for *D. pallidus* Coker but are abundant in the new species (fig. 10).

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BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 81, NO. 4, PP. 304–312 JULY, 1954

CERTAIN CYTOKINETIC FACTORS IN LIVING EPIDERMAL CELLS AS ILLUMINATED BY THREE DIMENSIONAL CELL-SHAPE STUDIES OF PHLEUM PRATENSE ROOTS[1]

HUGH NELSON MOZINGO

Using a large and diverse group of tissues, various workers have obtained results from cell-shape studies which indicate their considerable value as a tool in unraveling the complexities of morphological development in the plant.

The present investigation is concerned with the cell-shape characteristics of fully matured and differentiated epidermal cells in the roots of *Phleum pratense* seedlings. It is a logical continuation of cell-shape studies initiated by Matzke (1939, 1945), and is intended as a supplement to previous work on youthful cells located in a more distal position on the roots of this particular plant. A previous paper (Mozingo 1951) reviewed the pertinent literature with regard to this particular tissue. This earlier study showed that not only in the last division (Sinnott & Bloch, 1939a and b), but also in the preceding divisions a pronounced tendency for the epidermal cells of the root meristem to divide unequally exists; with the result that the cell plate becomes displaced towards the apical end of the cell.

Materials and methods. The technique used in germinating the grains of *Phleum pratense* was substantially the same as that used in the earlier study. In similar fashion, the roots were examined and cell-shape determinations were made with the roots in a living condition.

The primary roots used in these examinations averaged 16.2 mm. in length. The cells examined were located from 0.85 to 23 mm. from the root apex, well into the "zone of maturation." A camera lucida was used to record the outer faces and lateral contacts of the cells; basal contacts were, of necessity, added without the aid of this device. Examinations were restricted to obvious pairs of cells derived from a single parent cell. These pairs included a distal (trichoblast) and a proximal (non-trichoblast) cell, with the latter as the larger member of the pair as a result of the inequality of the last division.

Results. Table 1 gives the range and number of facets in the 200 cells observed; the average number of faces for the entire group being 10.45. Because this average includes two quite distinct populations, it would, perhaps, be more precise to consider each of these groups separately.

[1] The author would like to express his appreciation to Professor Edwin B. Matzke of Columbia University for his constructive criticisms, and to his wife, Katherine W. Mozingo, for her help in the preparation of the manuscript for publication.

The 100 distal or "trichoblast" cells had an average of 9.44 ± 0.12 faces. All of these cells had developed root hairs. The range was from 7–13 faces with 89 out of the 100 cells having either 8, 9, 10 or 11 facets. The ratio of outer: lateral: basal faces was approximately 1:5:3, with pentagons most

TABLE 1. *Number of faces in 100 distal and 100 promixal cells in Phleum root epidermis.*

No. of faces	Number of Distal cells	Total faces	Number of Proximal cells	Total faces
7	5	35		
8	25	200	2	16
9	23	207	8	72
10	22	220	18	180
11	19	209	24	264
12	5	60	24	288
13	1	13	11	143
14	—	—	12	168
15	—	—	1	15
Totals	100	944	100	1146
	Average no. of faces $\frac{944}{100} = 9.44$		Average no. of faces $\frac{1146}{100} = 11.46$	

abundant among the outer faces (table 2). The average number of sides to the outer faces was 5.25. The most common combination of facets, 4–4, occurred 22 times (table 4). This was over twice as common as the next most abundant combination, 4–4–1, which occurred only 10 times.

TABLE 2. *Distribution of kinds of faces in 100 distal cells in Phleum root epidermis.*

	Number of sides per face							Total faces
	3	4	5	6	7	8	9	
Outer faces:	—	21	40	33	5	1	—	100
Lateral faces:	1	215	295	13	1	—	—	525
Basal faces:	12	133	103	62	9	—	—	319
							Total:	944

Average number of sides to outer faces $= \frac{525}{100} = 5.25$

The 100 proximal cells were found to have an average of 11.46 ± 0.156 faces. The number ranged from 8 to 15 faces with 89 of the 100 cells having either 10, 11, 12, 13 or 14 faces. The ratio of outer: lateral: basal faces approximated 1:6:4, with hexagons predominating among the outer faces (table 3). The outer faces had an average of 6.41 sides. In this group the

most abundant combination was 3–6–2, which occurred 12 times in the 100 cells (table 4). The combinations 3–7–1–1 and 4–4–2 followed, each being found 7 times.

TABLE 3. *Distribution of kinds of faces in 100 proximal cells in Phleum root epidermis.*

	Number of sides per face								Total faces
	3	4	5	6	7	8	9	10	
Outer faces:	....	1	15	42	30	9	2	1	100
Lateral faces:	2	248	365	26	1	....	....	....	642
Basal faces:	13	108	148	110	24	1	....	....	404
								Total:	1146

$$\text{Average number of sides to outer faces} = \frac{641}{100} = 6.41$$

Typical pairs of distal and proximal cells are diagrammed in figure 1.

Only 27 different combinations occurred among the distal cells contrasted to the 40 combinations which occurred among the proximal cells.

Discussion. The results obtained for both the distal and proximal cells (1:5:3 and 1:6:4 respectively) indicate that the number of basal facets is significantly greater than would be expected on the basis of earlier studies on immature cells. The proximal cells here had an average of 4.04 basal faces. The 78 proximal "interphase" cells of the earlier study just before division, when the greatest number of contacts would be present, had an average of 3.46 basal faces, a figure which does not significantly approach the high average obtained in the present study.

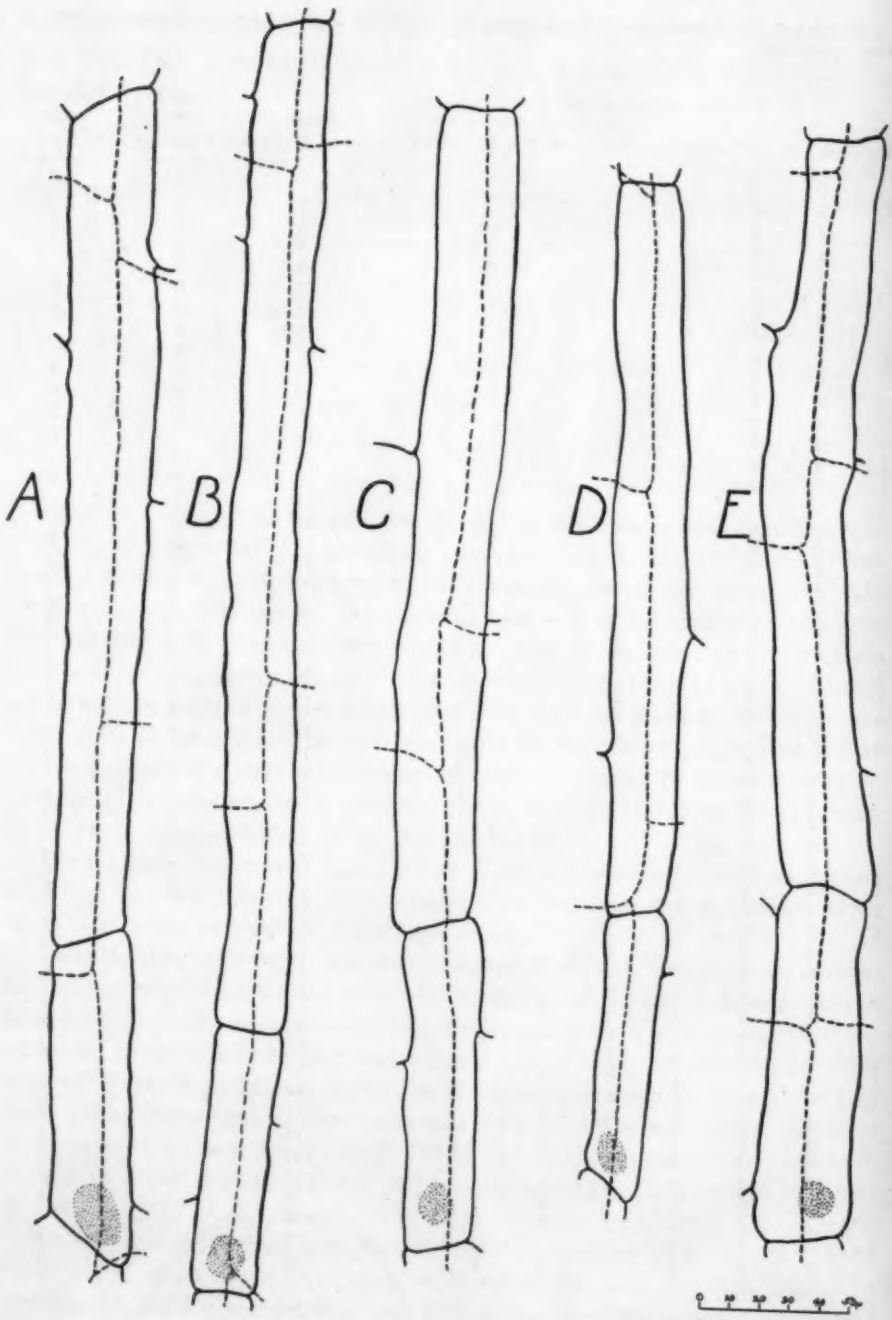
This higher number of basal contacts obviously results from continued divisions in that layer of cells immediately beneath the epidermis after divisions in the superficial layer have ceased.

Despite this difference, it seems probable that both tissues cease elongation at the same time, since continued elongation of the subepidermal tissues would result in the separation of the epidermal cells. The obvious interpretation to be drawn from this last observation is that the interval between the last division and the termination of elongation must be shorter in this underlying tissue than in the epidermal cells. Along related lines, Goodwin & Stepka (1945) and Esau (1938, 1943a and b) have pointed out that with regard to other tissues, phloem differentiates sooner than xylem in plant meristems.

Ideally, the epidermal cells should have an average of 11 facets (Lewis 1943, 1949) when the subepidermal cells are of the same size. The combined average of 10.45 observed here would indicate that the subepidermal cells are somewhat larger than those of the epidermis. However, if only the proxi-

TABLE 4. *Combinations of faces found in 100 distal and 100 proximal cells in Phleum root epidermis.*

Number of sides per face								Faces	Distal cells (No.)	Proximal cells (No.)
3	4	5	6	7	8	9	10			
	5	2						7	5	
	3	4	1*					8	1	
	4	4						8	22	2
	6	0	2					8	1	
1	3	3	1					8	1	
	3	6						9	6	2
	4	4	1					9	10	6
	5	2	2					9	4	
1	3	3	2					9	3	
	2	8						10	6	1
	3	6	1					10	6	6
	4	4	2					10	6	7
	5	3	1	1				10		2
1	3	3	3					10	1	
1	3	4	1	1				10	1	2
1	4	1	4					10	1	
1	4	2	2	1				10	1	
	2	8	1					11	2	2
	3	6	2					11	8	12
	4	4	3					11	4	4
	4	5	1	1				11	1	2
	5	4	0	2				11		1
	6	3	0	1	1			11		1
1	2	5	3					11		1
1	3	5	0	2				11		1
1	4	2	3	1				11	3	
1	5	1	2	2				11	1	
	3	6	3					12		3
	3	7	1	1				12		7
	4	4	4					12		3
	4	5	2	1				12	2	4
	4	6	0	2				12	1	
	5	4	1	2				12	1	1
1	3	4	3	1				12	1	3
1	4	3	2	2				12		2
2	2	5	2	1*				12		1
	3	7	2	1				13		2
	4	5	3	1				13		2
	4	6	1	2				13		2
	4	6	2	0	1			13	1	2
	5	4	2	2				13		1
1	2	6	3	1				13		1
1	4	5	1	0	2			13		1
	3	7	3	1				14		3
	4	6	3	0	1			14		3
	4	7	1	1	1			14		1
	5	4	3	2				14		1
	5	4	4	0	1			14		1
	5	6	1	1	0	1		14		1
	6	5	1	1	0	0	1	14		1
2	1	7	1	3				14		1
	5	6	2	1	0	1		15		1
Totals:									100	100


A
B
C
D
E

mal or non-trichoblastic cells are taken into consideration with their average of 11.46 faces, it seems obvious that they must be larger in at least one dimension (i.e., length) than the subepidermal cells.

Matzke (1947) found that the epidermal cells on the leaves of *Aloe aristata* had an average of 10.88 faces, a figure indicative of only slightly larger subepidermal cells. However, the same author (Matzke 1948) found that epidermal cells on the apical meristem of *Anacharis densa* had an average of only 10.005 faces. This was due to the noticeably larger subepidemal cells.

In the preceding study it was postulated that the "middle" interphase average should be approximately 10.34. If allowance is made for the continued cell divisions in the subepidermal layer (as evidenced in the present study), this figure is suitably close to the observed average of 10.45.

The very significant difference in the average number of faces of trichoblast (9.44 ± 0.12) and hairless cells (11.46 ± 0.156) indicates, as Sinnott & Bloch (1939a and b) have shown for this same tissue in *Phleum*, that the last division leading up to their formation was decidedly unequal.

In the author's early study (1951) it was found that an average of 2.18 contacts was added during the total interphase period.

Because of the random nature and, particularly, the non-simultaneity of cell division in the root tip it would, perhaps, be illogical to suppose that mature cells represent cells at either one extreme (immediately after division) or the other (just before division) of interphase. Stated in other terms, any cell upon dividing must necessarily raise the number of contacts in at least several of its neighboring cells. If division then ceases and this cell along with its neighbors proceeds to mature, it can be said that the two cells produced by the last division (now undergoing maturation) represent cells in the most youthful interphase condition, as far as the number of facets each possesses is concerned. However, the neighboring cells affected by this division will, as far as contacts are concerned, be in an intermediate interphase condition, even if they have just completed divisions themselves prior to the division of the cell in question. Since a significant portion of these cells would be expected, on the basis of chance, to have experienced this situation twice, and thereby to have attained a "mature" or "old" in-

FIG. 1. Five typical pairs of distal (trichoblast) and proximal (non-trichoblast) cells. The distal cells and the apex of the root are towards the bottom. The stippled areas represent the points of origin of root hairs. Dotted lines represent the basal contacts. Combinations of facets: *A. Distal cell*, 1-triangular, 3-quadrilateral, 4-pentagonal, 1-hexagonal, 1-heptagonal; *Proximal cell*, 4-quadrilateral, 6-pentagonal, 1-hexagonal, 2-heptagonal. *B. Distal cell*, 4-quadrilateral, 4-pentagonal, 2-hexagonal; *Proximal cell*, 3-quadrilateral, 7-pentagonal, 3-hexagonal, 1-heptagonal. *C. Distal cell*, 4-quadrilateral, 4-pentagonal, 1-hexagonal; *Proximal cells*, 3-quadrilateral, 6-pentagonal, 2-hexagonal. *D. Distal cell*, 4-quadrilateral, 4-pentagonal; *Proximal cell*, 1-triangular, 2-quadrilateral, 6-pentagonal, 3-hexagonal, 1-heptagonal. *E. Distal cell*, 3-quadrilateral, 6-pentagonal, 2-hexagonal; *Proximal cell*, 4-quadrilateral, 5-pentagonal, 3-hexagonal, 1-heptagonal.

terphase condition before maturing, it may be assumed with some assurance that the mature cells represent cells in an "intermediate" interphase condition. The trichoblast cells herein reported upon should have had upon formation approximately one-half of the total probable added contacts (i.e., $\frac{218}{2} = 1.09$) less than the reported average; i.e., $9.44 - 1.09 = 8.35$. This last figure, then, we can assume represents the average number of faces present in the trichoblast cells immediately after the division that produced them.

If this figure (8.35) and the two averages obtained in the previous study for the parent and daughter distal (potentially trichoblastic) cells (8.97 and 8.64 respectively) are plotted, it will be seen that the points fall along a remarkably straight line (fig. 2). Presumably, this would indicate that there

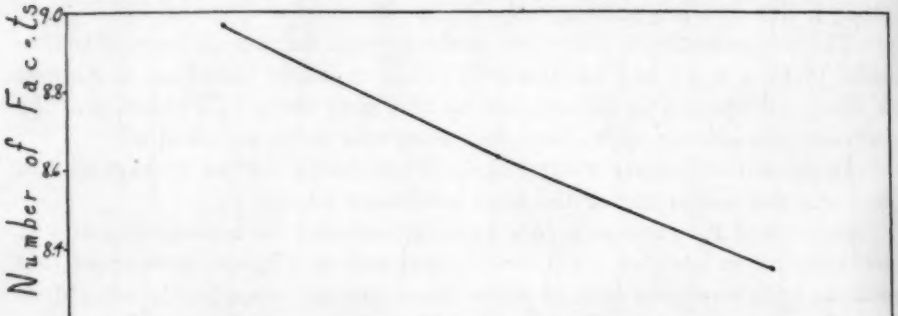


FIG. 2. Graph illustrating the progressive tendency, from the distal to the proximal region of the meristem, towards the production of fewer-faceted, potentially trichoblastic, epidermal cells. A. "Parent" distal cells. B. "Daughter" distal cells. C. Distal cells of present study. (See text for further explanation.)

is some unknown morphogenetic factor or factors causing these cells to divide unequally; the influence of this factor is apparent well into the meristem and its effects show a constant increase to a maximum point at the last division.

The average number of sides to the outer faces was widely divergent, as would be expected, with the distal cells having an average of 5.25 sides and the proximal having an average of 6.41 sides. The combined average of 5.83 is somewhat closer to the ideal of 6.

Also, as would be expected, the distal cells had 8 faceted cells as the predominant type, while the proximal cells had 11 and 12 faceted kinds sharing equally the role of the predominant type.

There were many more combinations (40) among the proximal cells than among the distal cells (27). This, most probably, is due to the larger proportionate size of the proximal cells.

The most common combination, 4–4, occurred 22 times among the distal cells but only twice among the proximal cells where the most common combination was 3–6–2, occurring 12 times.

The combination 4–4–2, which was the most abundant among 200 epidermal Elodea cells (34 times, Matzke 1948), occurred 6 times among the distal cells and 7 times among the proximal cells. However, the combination 3–6–2, which occurred 34 times in 200 epidermal cells of *Aloe aristata* (Matzke 1947), as has already been pointed out, was also the most common combination among the mature proximal *Phleum* cells.

Tetrahedral angles occurred in 2 instances. These are marked with an asterisk in table 4.

Several conclusions may be drawn from the foregoing data. The most significant of these is the tendency displayed throughout the meristem for the epidermal cells to divide unequally. This trend becomes most exaggerated during the last division.

Perhaps additional cell-shape studies on this tissue combined with certain experimental techniques may throw more light on the unknown causative factor.

Secondly, the subepidermal cells appear to continue their divisions for a significant period after the epidermal cells have ceased dividing.

Thirdly, except as influenced by the above mentioned factors and the usual anticlinal nature of the new dividing wall, there appears to be no set pattern during cell division. This is reflected in the multiplicity of combinations observed.

Finally, the mature epidermal cells show a considerable number of similarities to epidermal cells in *Elodea* and *Aloe*. The disparities present may be accounted for by those characteristics peculiar to *Phleum* root epidermal tissue. Under the conditions of this study no proximal cells were observed to have produced root hairs. However, it has been shown that other environmental circumstances will bring about the production of root hairs by these cells (Cormack 1944).

SUMMARY

1. The cell shapes of mature epidermal cells in the roots of *Phleum pratense* were determined for 200 cells.

2. These 200 cells consisted of 100 pairs of trichoblastic or distal cells and non-trichoblastic or proximal cells.

3. The distal cells were found to average 9.44 facets, while the proximal cells averaged 11.46 facets. Pentagonal, quadrilateral, and hexagonal facets were most abundant in that order among both the distal and proximal cells.

4. The distal cells occurred in 27 combinations; the proximals, in 40 combinations.

5. The commonest combination among the distal cells was: 4 quadrilaterals, 4 pentagonals.

6. In the proximal group the commonest combination was: 3 quadrilaterals, 6 pentagonals, 2 hexagonals.

7. Correlation of the results obtained here with those of a preceding study indicates that the cells of the subepidermal tissue continue to divide after divisions have ceased in the epidermal layer.

8. In addition, the earlier work together with the present study indicates a trend existing throughout the meristem for the epidermal cells to divide unequally with the cell plate displaced to the distal end of the cells. This trend reaches its maximum extent during the last division.

9. It appears that, except as influenced by the obvious restrictions present in this tissue, cell shape is here influenced by a complex network of partially unknown interacting physicochemical factors.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 81, NO. 4, PP. 313–322 JULY, 1954

A STUDY OF RIBOFLAVIN, THIAMINE, NIACIN AND ASCORBIC ACID CONTENT OF PLANTS IN NORTHERN ALASKA[1]

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Chemical investigations of arctic plants are very few. Therefore the opportunity offered under a grant from the Arctic Institute of North America, to study the vitamin content of north Alaskan plants, was greatly appreciated. Arrangements were made with the Office of Naval Research to use the facilities of its Arctic Research Laboratory located at Point Barrow Base Camp, for collecting and processing the plant material preliminary to the analyses. The stay at the Point Barrow Base Camp extended from August 21 to September 11, 1951. This was a little late in the season and many plants were through their blossoming period, and some had even completed their growth for the season, but there were still available a number of plants that were growing actively and of these thirty-two species were collected. Up to the time of departure there had been no killing frost.

In 1933 Ellis, Palmer and Barnum made a study of vitamin B (thiamine) and G (riboflavin) in lichens from Alaska. Feeding tests with rats failed to show the presence of these two vitamins in any of the twenty-two species they studied. Rodahl (1945) also made a study of thiamine, in plants from North-East Greenland. He determined the thiamine by the thiochrome method. To preserve the vitamin until analyses could be made he prepared a hydrochloric acid extract of the plant material and adsorbed the vitamin on "Francomit" which at the time of analyses was eluted with an alkaline solution. Rodahl investigated twenty species of plants. The thiamine content varied from a trace in *Cassiope tetragona* to 3.50 micrograms per gram plant material in willow buds. Aside from the values for the willow buds and stems the content was considerably below one microgram per gram.

Höygaard and Rasmussen (1939) investigated the ascorbic acid content of foodstuffs of the Eskimos around Angmagssalik, South-East Greenland and they found this vitamin high enough to prevent scurvy. They report that *Sedum roseum* had a concentration of 27 mg. per 100 g. of fresh plant material, *Salix* sp. 18 mg., dandelion 15 mg., and several other higher plant

[1] Paper from the Department of Botany of the University of Michigan, No. 970. The writer wishes to express his thanks to the Arctic Institute of North America from whom a grant-in-aid was received, and to the Office of Naval Research, which supplied the facilities at Point Barrow Base Camp. Dr. I. L. Wiggins, Director of the Arctic Research Laboratory, and his staff also contributed much to the success of the collecting and processing of the material.

species ranging a little lower. A few species of marine algae were also studied and they found the brown alga *Alaria* sp. to contain 45 mg. per 100 g. of plant and the red alga *Rhodymenia palmata*, eaten extensively by Orientals, contained 17 mg. per 100 g. Rodahl (1944) determining the ascorbic acid in a number of plants, found that there was a large seasonal variation in such plants as *Honckenya peploides* and *Betula nana* whereas *Salix* sp. showed only a slight variation in the stems and buds. He points out that the musk ox and ptarmigan feed extensively on the willow. The range in ascorbic acid content is very great, from a few milligrams in *Papaver radicatum* to 314 mg. per 100 g. in *Potentilla nivea*. Comparing his findings from North-East Greenland with those of Höygaard and Rasmussen from South-East Greenland, he finds a higher ascorbic acid content at the higher latitude (74° 30′ N.). This is very interesting because Rostenko (1943) and Zepkova (1945) found, in Asia, that with increase in altitude at which the plants grew there was likewise an increase in the ascorbic acid content.

In recent years the Alaska Department of Health and the Alaska Experiment Station have been making ascorbic acid determinations on many wild plants and some cultivated plants. Unfortunately this work has not yet been published, except for preliminary reports by Shepard (1948 and 1950) and Heller (1949). These show that the ascorbic acid varies greatly in the plants analyzed, ranging from zero for such plants as *Ledum groenlandicum* to 1400 mg. per 100 grams fresh weight for rose hips. In between are *Salix pulchra* 544 mg., *Rumex acetocella* 420 mg., *Cochlearia officinalis* 175 mg., and *Picea mariana* needles 90 mg.

The Alaskan workers do not state methods used to preserve the plant material from the time of collection to the time of analyses, nor the methods of analyses. The quantity of ascorbic acid for the same plant varies also greatly from report to report. This can partly at least be due to different times of the year and different localities from which the plants came. They draw no conclusion as to the influence of the environment.

Methods of preserving the material. The problem of preserving the vitamins in the plants for future analysis was a perplexing one. A few months previously the writer had successfully shipped plant material packed in dry ice from Pasadena, California, to Ann Arbor, Michigan, by air. This method of taking care of the material was seriously considered but it was found to be impractical. Drying the plants rapidly at 60° C. had been tried and found to be unsatisfactory. In recent years, enzymologists have prepared their material by lyophilization, i.e., by drying the material at very low air pressure and at near-zero degree temperature. This method of preparing the material was finally decided upon and the problem of getting the low temperature necessary was solved by using dry snow

produced by allowing CO_2 to escape into a paper carton from a tank. This method of processing the plant material proved to be very successful.

As soon as the plants were collected they were, for the most part, lyophilized at once, but sometimes more material was collected than could be processed immediately and this was stored in a deep-freezer, at about – 20° C., until it could be dried. This low temperature storage had previously been found not to influence the thiamine, riboflavin and niacin content adversely. Gustafson and Cooke (1952) have shown that this low temperature treatment previous to the lyophilization oxidizes the ascorbic acid to the dehydroascorbic acid, and for this reason only the total ascorbic acid is given in this report; it is not adversely influenced by the low temperature storage previous to the lyophilization. As soon as the plants were dry they were placed in screw-top plastic tubes and sealed tightly with a preparation called "Alvar," used by archeologists to preserve their specimens. The plants were brought to Ann Arbor by plane and stored in a deep freezer at – 20° C. until used.

The plant material. As an aid to future investigators and others interested in the nutritive values of Arctic plants a brief description will be given of each plant species tested and of conditions under which it grew, at or near Point Barrow; mention will also be made of the part that was used. Figure 1 gives a good idea of the nature of the terrain on which most of the plants were collected.

Alopacurus alpinus is a very common grass on the tundra. Fruiting stems and leaves were used in the three collections made.

Arctagrostis latifolia is another grass common on the tundra but the material used was collected on dry soil at the mouth of a drainage ditch. The plants were very luxuriant. Two collections were made, one of young vegetative plants and another of older plants with fruiting stems and leaves. As the table shows the flowering plants are somewhat richer in vitamins than are the more luxuriant vegetative plants.

Arctophila fulva is also quite a common grass in low moist places on the tundra. It was collected near the old excavation of an Eskimo house at Birnik. The soil was very rich due to the drainage from the excavation, and the plants extraordinarily luscious; only vegetative parts were used. As seen in table 1, the vitamin content of this grass is higher than that of the other grasses and this may be due to rich soil in which it grew and consequently its greater vigor.

Cassiope tetragona grows on the dry tundra and is not very common at Point Barrow, but reported to be very common farther south. Eskimos use it as fuel and call it Pi-a-ra-ra. Only green tips about half an inch long were used and this was all probably the current season's growth.

Cerastium Beeringianum grows on the shores of lakes or drainage

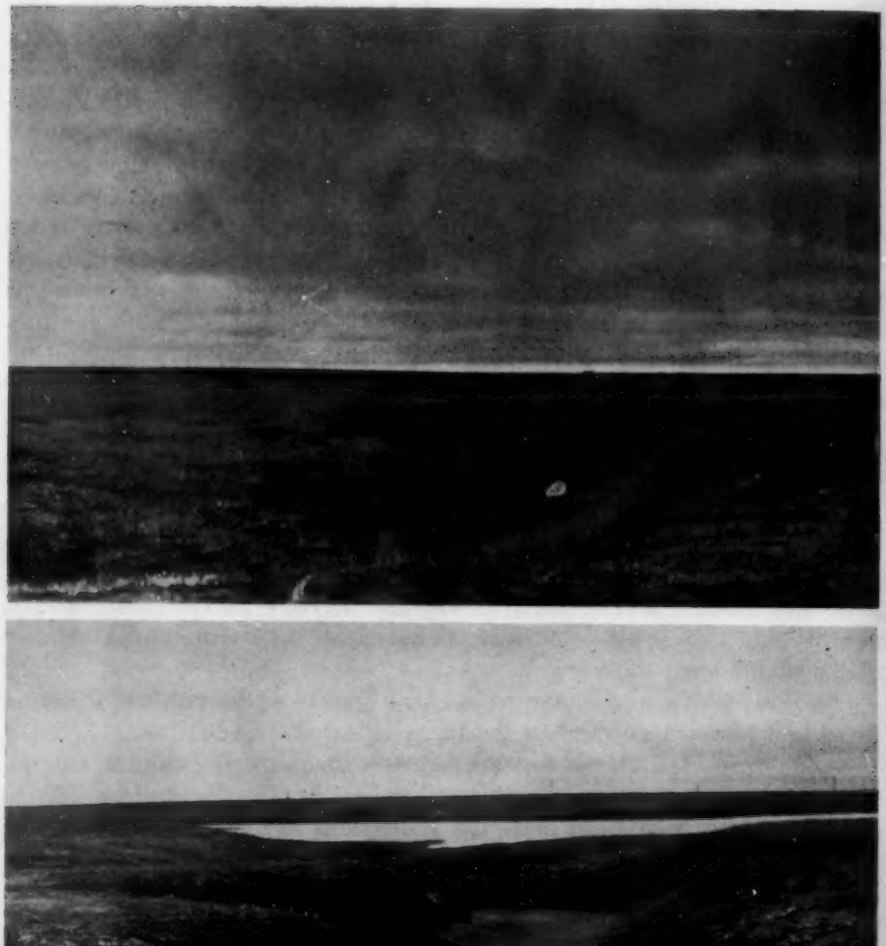

FIG. 1. Tundra near Point Barrow Base Camp, Alaska.

ditches. Material used was in flower and whole plants were used.

Chrysosplenium tetrandrum is a plant only a few inches tall and it was found in moist places and in drier areas where the soil had been enriched by bones and horns of caribou. Whole plants were used.

Cetraria delisei and *Stereocaulon* sp. are two species of lichens fairly common on old lake beaches. The two species commonly grow together.

Cochlearia officinalis ssp. arctica (Scurvy plant) is found in moist places scattered widely but at no point very abundant. The rosette leaves from plants in bloom or nearly ready to blossom were used. As the common name indicates its use is considered to be a preventative against scurvy. Yet ascorbic acid is not as high as it is in some other plants analyzed.

Dryas integrifolia was collected only once, at Nunavak, some 10 miles from the camp on rather high and dry ground. The plants were in fruit but only the leaves were used.

Dupontia Fisheri is a grass that grows on lake shores or other wet places. The plants analyzed were collected at Ikrowik and were in excellent vegetative condition.

Eriophorum angustifolium and *E. Scheuchzeri* are very abundant and in early September the tundra was, in places, white from the fruiting parts. Only green vegetative shoots were used from very wet habitats where they were not fruiting. According to D. Q. Thompson (private communication) these species form important foods for the brown lemming.

Oxyria digyna is found in restricted areas. The material used was collected on an old lake shore. Only rosette leaves of fruiting plants were used.

Papaver radicatum which is quite common on high frost ridges was in full bloom in late August. Only rosette leaves were used, from the flowering plants.

Petasites frigidus was quite common on the drier ground of the frost mounds. The plants were in fruit at the time of collecting. Young leaves and young tips of rhizomes were used. The next year's flower buds were also collected, but it was not possible to grind them because of high content of mucilage and hairs.

Potentilla hyparctica was very common on the drier, more or less barren frost mounds. By early September most of the plants were drying up, though enough rosette leaves, in good condition, were found for the analyses.

Pedicularis lanata was not a common plant, but abundant locally on low ground. The leaves used were basal ones, from fruiting plants.

Poa arctica was fairly common in moist places on the tundra. The basal part of vegetative plants was used.

Ranunculus nivalis was quite common in wetter areas. It was usually in fruiting condition, but the basal rosette leaves were still in very good condition.

Rumex articus was not very abundant but was found occasionally in draining ditches and other wet places. Before the advent of canned spinach the Eskimos used this plant as a green and called it A-ku-lo-pak. At the time of gathering the material, some leaves had turned completely red but others were still bright green. Analyses have been made separately of the two; the table shows that there is some loss as the leaves lose their chlorophyll, except for niacin, which has increased.

Salix phlebophylla, S. reticulata, S. Pulchra, and *S. rotundifolia* were all collected, but only the latter two were abundant. Almost every frost mound had an abundance of the trailing *S. rotundifolia,* while *S. pulchra* although less common was found quite frequently in moist habitats.

Saxifraga cernua, S. foliolosa, S. hieracifolia and *S. punctata* ssp. *Nelsoniana* were all collected and analyzed. All four species were in flower and fruit, but only the rosette leaves were used, and most of the *S. cernua* was collected from young rosettes not yet in blossom. All four species were common in the moister habitats.

Senecio atropurpureus was not widespread, but quite abundant on moist frost mounds. It was in blossom, but only the rosette leaves were used.

Stellaria laeta was quite common on low moist ground and sometimes even in running water. The latter condition is unusual. Two collections at widely separated regions were made. All plants were in flower and whole plants were used.

Vaccinium Vitis-Idaea ssp. *minus* was not abundant, but was frequently found on the drier frost mounds. No flowers or fruits were ever observed. Leaves were turning red, therefore both red and green leaves and stem tips were used. At this latitude the individual plants were one or two inches long.

Organic material. At three different places, soil in which our plants occurred was also collected for analyses. On the tundra where the *Salix* plants grew this material was probably a mixture of peat, humus and organic material. The soil in which *Saxifraga cernua* was rooted near the fresh water lake, is likely to be a mixture of humus and sand. The lower part of *Dicranum elongatum* is extensively finely decomposed material of the moss plus an accumulation of wind-blown silt.

Methods of analyses. The thiamine was determined by the thiochrome method and the riboflavin by a fluorescent method: both of which have been described by Connor and Straub (1944) and modified slightly by the writer (1947) for plant material. The niacin was assayed according to the method approved by the Association of Vitamin Chemists (1947), with *Lactobacillus arabinosus.* The ascorbic acid was determined by the 2,4-dinitrophenylhydrazine method proposed by Roe and Oesterling (1944).

Soon after the material reached Ann Arbor, it was ground in a small

Wiley mill to pass through a 60-mesh screen and placed in weighing bottles, in a deep freezer at −20° C. until needed. Twenty-four hours before they were made ready for analyses, the bottles were put in a vacuum desiccator over "drie-rite"; this gave a uniform basis on which calculations were made. Experiments with several species gave a figure for material maintained in the desiccator for 24 hours as about 10% dry weight, but this information is not too essential as all calculations are made on dry weight of material in the evacuated desiccator over "drie-rite."

For thiamine, riboflavin and niacin, 1 gram of dry powder was stirred up with 99 parts of water. With frequent stirrings this preparation was permitted to stand for 15 minutes, after which 50 ml. was measured out for thiamine and riboflavin assay and 40 ml. for niacin. From here on the procedure was according to the references given above.

For ascorbic acid analyses 0.3 gm. dry material was blended with 100 ml. of mixed acid and 1 g. thiourea in a Waring Blender for half a minute. From here on the procedure suggested by Roe and Oesterling for total ascorbic acid was followed.

Discussion and results. The results are given in table 1 as micrograms per gram dry material for thiamine, riboflavin an niacin, and ascorbic acid is given as milligrams per 100 gram of dry tissue. Each figure represents at least two different determinations and in some instances three.

In their work on lichens in Alaska, Ellis, Palmer and Barnum (1933), report that with the rat test neither vitamin B (probably thiamine) nor G (riboflavin) was present in their plants. In the present study two genera which they also studied were analyzed. It was found that both species contained all of the vitamins studied, but in quantities well below those found in the other plants. While this study does not agree with Ellis, Palmer and Barnum, that there is no thiamine and riboflavin in lichens, it certainly, however, brings out the fact that the low vitamin content of lichens does not supply the animals feeding on them with all the vitamins they need.

Of six species studied both by Rodahl and the writer, *Dryas, Papaver, Cassiope* and *Alopecurus* had a much higher thiamine content in Alaska than in Greenland, whereas in *Oxyria* and *Saxifraga cernua* there was not much difference in the two places. Of three other genera, but different species, studied by both investigators, two had a higher thiamine content in Alaska, and one was higher in Greenland.

Ascorbic acid was studied by both investigators in five identical species and of these four had a much higher ascorbic acid content in Greenland and only one was higher in Alaska. In some genera where species studied were different in the two regions, there was some difference, and sometimes this was in favor of one region and sometimes in favor of the other. Most

TABLE 1. *Riboflavin, thiamine, niacin and ascorbic acid content of some north Alaskan plants. Vitamin content calculated on the basis of dry weight.*

Name of plant	Riboflavin mcg/g	Thiamine mcg/g	Niacin mcg/g	Ascorbic acid mg/100 g
Alopecurus alpinus (Gramineae)	9.8	2.4	29.2	190
Arctagrostis latifolia (Gramineae)				
young leaves	11.2	3.6	42.4	208
flowering stems & leaves	14.3	3.5	55.1	305
Arctophila fulva (Gramineae)	15.4	5.0	62.7	358
Cassiope tetragona (Ericaceae)	7.5	1.6	31.3	61
Cerastium Beeringianum (Caryophyllaceae)	11.4	5.2	117.7	102
Chrysosplenium tetrandrum (Saxifragaceae)				
basal leaves	10.8	3.2	111.2	200
fruiting stems	9.1	2.6	141.9	515
Cetraria delisei (Lichen)	4.1	0.9	22.9	57
Cochlearia officinalis ssp. arctica (Cruciferae)	13.8	7.4	55.6	396
Dryas integrifolia (Rousaceae)	11.9	3.5	44.4	105
Dupontia Fisheri (Gramineae)	14.1	4.3	54.1	198
Eriophorum angustifolium (Cyperaceae)	12.8	2.9	36.5	314
Eriophorum Scheuchzeri (Cyperaceae)	14.2	3.7	45.4	236
Oxyria digyna (Polygonaceae)	11.7	5.8	84.7	585
Papaver radicatum (Papaveraceae)	18.2	4.6	54.9	193
Pedicularis lanata (Scrophulariaceae)	15.5	2.0	58.2	343
Petasites frigidus (Compositae)				
leaves	14.2	4.8	81.0	279
young rhizomes	4.7	3.4	60.0	42
Poa arctica (Gramineae)	12.7	2.6	39.8	326
Potentilla hyparctica (Rosaceae)	14.4	2.5	68.2	748
Ranunculus nivalis (Ranunculaceae)	18.3	5.7	112.8	286
Rumex arcticus (Polygonaceae)				
green leaves	13.5	5.8	81.8	382
red leaves	11.4	4.7	113.1	303
Salix phlebophylla (Salicaceae)	12.2	3.8	49.7	615
Salix pulchra (Salicaceae)				
leaves	12.7	1.5	49.4	382
current year's stem	5.4	2.2	30.4	189
Salix reticulata (Salicaceae)	12.5	4.8	32.5	462
Salix rotundifolia (Salicaceae)				
leaves	11.1	4.4	58.3	432
fruits	6.1	2.9	23.5	138
Saxifraga cernua (Saxifragaceae)	12.8	2.5	74.2	413
Saxifraga foliolosa (Saxifragaceae)	15.5	3.7	125.3	625
Saxifraga hieracifolia (Saxifragaceae)	9.9	0.9	64.1	796
Saxifraga punctata ssp. Nelsoniana (Saxifragaceae)	12.5	2.4	64.7	681
Senecio atropurpureus (Compositae)	12.1	3.4	70.2	174
Stellaria laeta (Caryophyllaceae)	15.5	6.1	65.0	330
Stereocaulon sp. (Lichen)	5.2	1.8	27.6	82
Vaccinium Vitis-Idaea ssp. minus (Ericaceae)				
green leaves and stem	10.5	2.1	32.2	233
red leaves and stem	10.3	4.3	94.4	295
Organic Matter (Salix plants grew in this)	2.2	0	8.5	20
Organic Matter (Saxifraga cernua grew in this)	3.1	0	10.8	15
Organic Matter (lower part of decomposing Dieranum elongatum)	1.5	0	5.0	21

of Rodahl's analyses were made in June or July but this did not materially influence the results.

No direct comparison can be made between the results reported here and those of Shepard (1950), because she did not use the same species or even genera of plants but aside from the rose hips all of her results are much below those given in this report. Heller's figures for *Rumex arctica*, *Salix pulchra* and *Cochlearia officinalis* are higher than those reported here. In 1948 Shepard published a list of cultivated Alaskan plants with their ascorbic acid content. Unfortunately she does not indicate what part of the plants were analyzed but if the figures given are used, the wild plants of the Barrow Region compare very favorably with the cultivated plants of Alaska.

In examining the table one notices one fact, namely that the riboflavin content ranges around the values 11.0 to 14 micrograms per gram dry material, with some exceptions below and above. This is in contrast to the large variation in all of the other vitamins.

In attempting to account for the wide range in thiamine content, the method of preparing and storing the material has been carefully checked. Several experiments with tomato leaves were performed; some were lyophilized and stored for as long as 54 days and others used fresh. The lyophilizing process itself does not destroy any of the vitamins studied and a storage of 54 days at the temperature of $-20°$ C. does not either. The material collected at Point Barrow was stored for a longer period than this but the first determinations were made within two months after collecting and preparing the material and there were no essential differences between the first and later analyses.

There is no family or larger group of plants that is outstanding either because of low or high vitamin content; when several species of a genus are analyzed as *Salix* and *Saxifraga* some species may be high in a particular vitamin and others quite low. The exceptions to the above statement are the two genera of lichens, which are both very low. In two instances where fruiting plants were compared with vegetative plants, the fruiting ones were higher in the ascorbic acid and niacin than the vegetative plants. Frequently the statement is made that soil, especially soil composed largely of organic material, is rich in vitamins, but that certainly is not true for the three samples analyzed from the Barrow Region.

Summary

1. The thiamine, riboflavin, niacin and ascorbic acid content has been determined in 32 species of plants collected at the Point Barrow Base Camp, Alaska. All plants contain these vitamins, though the two species of lichens were very low in all of them.

2. Riboflavin is quite high and for most plants is around 11.0 and 14.0 micrograms per gram of dry material, but all the others vary greatly in the species studied.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 81, NO. 4, PP. 323–328 JULY, 1954

PHOTOPERIODISM IN RICE. I. PHOTOPERIODIC RESPONSE OF ONE VARIETY OF DALUA (SPRING) RICE

GADADHAR MISRA

In Orissa there are nearly 28,000 acres of land under Dalua paddy, chiefly in the districts of Cuttack and Puri, where there are vast low lying areas. There are shallow depressions where water accumulates during the monsoon. In these parts the water level gradually falls by evaporation and by the end of November, lands fit for Dalua cultivation start emerging slowly. Cultivation starts on the periphery and moves towards the centre as more lands come out. The sowing commences generally in December and continues up to February. Harvest commences in March and continues to May. The varieties cultivated are generally coarse, having red rice. There is a strong belief that no other variety except the usual two or three varieties of paddy grown in these areas, could be cultivated as Dalua. As a result of researches carried out in the Department of Agriculture, Orissa, a number of selections from natural hybrids in a Japanese variety "Orosporzes" have successfully been evolved and introduced in these Dalua areas (Dixit 1944).

The scope of vernalisation and photoperiodism in Indian agriculture has been discussed by Sircar (1948). The possibilities of applying this technique to rice is yet to be explored in great detail. In India the photoperiodic work on rice is confined mostly to three states, e.g. Bihar, Bengal and Uttar Pradesh. In Bihar, Saran (1945) investigating five pure varieties of rice came to the conclusion that by application of short days any variety of paddy irrespective of the class or maturity period to which it belonged, could be induced to flower within 60–63 days of germination. In a later work (1950) he has reported that the minimum effective period of short days to bring about early flowering is 15 days. In Bengal, Sircar (1946), Sircar & Parija (1949) obtained great acceleration in flowering in three varieties of winter rice, "Bhasamanik," "Rupsail" and "Patnai." In U. P., Misra (1950) obtained earlier flowering in two varieties of late rice by application of short days at different ages of the seedlings. Since the photoperiodic response of rice greatly varies with varieties, an attempt has been made here to determine the photoperiodic response of one Dalua (spring) rice grown in Orissa. A preliminary brief report was published earlier (Misra 1953).

Material and methods. Of the several recommended types, type D.I.4 forms the material of the present investigation. The paddy is straw coloured. The grains are long and lighter in shade. Rice is white and of good quality. This experiment aims at the effect of short as well as long days on

the Spring variety of rice, viz., D.I.4 of Orissa. Two short-day treatments were given, viz., one having an 8 hour photoperiod and the other a 10 hour photoperiod. The seedlings which received these treatments till ear emergence were one or two weeks old at the time of the commencement of the treatments. The long-day treatment consisted of 24 hr. daily exposure to light. Here the seedlings receiving treatments were one week old and the treatment lasted for 20 days in one set and 30 days in another.

Experimental results and discussion. The records on ear emergence, grain yield and components of yield are recorded as usual and are presented below.

TABLE 1. *Time from sowing to ear emergence of the main shoot. Sowing date, 2-19-1949. Transplanting date, 3-18-1949. + indicates earliness; – indicates delaying effect.*

Treatments	Average No. of days from sowing to ear emergence	Difference from control in days
S. Day of 8 hrs. from 1st week till ear emergence	87.51	+ 129.35
S. Day of 8 hrs. from 2nd week till ear emergence	86.63	+ 130.23
S. Day of 10 hrs. from 1st week till ear emergence	88.13	+ 128.73
S. Day of 10 hrs. from 2nd week till ear emergence	83.68	+ 133.18
L. Day of 24 hrs. from 1st week for 20 days	215.85	+ 1.01
L. Day of 24 hrs. from 1st week for 30 days	213.03	+ 3.83
Control	216.86	

S. E. Mean = 2.36; C. D. at 5% = 6.77.

Time of heading. Date for ear emergence are presented in Table 1. The analysis of variance of the data is given in Table 2.

TABLE 2. *Analysis of Variance*

Source of Variation	D. F.	S. S.	M. S.	F.	5% F.	1% F.
Between treatments	6	170,641.00	28,440.18	849.97**	2.37	3.36
Within treatments	35	1,171.19	33.46			
Total	41	171,812.29				

** Significant at 1% level.

Normally when this variety is sown in December or January in Orissa it takes 90–100 days to flower. Obviously it flowers when the photoperiod is near 12 hrs. It is classified, therefore, as a spring paddy in Orissa equivalent in status to the Boro paddy of Bengal and Uttar Pradesh. In the present investigation the sowing date has been a little delayed, i.e., February 19, and transplanting has been done on March 18. The venue of cultivation has also shifted from a southern latitude, Cuttack (20° 28′ N.) to that of a northern latitude, Allahabad (25° 28′ N.). As a result of the

exposure of one and two week old seedlings of D.I.4 to 8- and 10-hour photoperiods it is seen (Table 1) that short days have brought about ear emergence in 83–88 days. There is no significant difference between the effects of the two periods of day lengths used. Short-day treatment appears to be slightly more effective when applied to the two-week-old seedlings than the one-week-old seedlings. Treatment of one-week-old seedlings with 24 hr. long days for 20 and 30 days has no marked difference from the control plants. The control plants, on the other hand, did not come to ear until 7 months had elapsed. Since no anatomical work has been done with the growing apex, it cannot be said with certainty whether the change from the vegetative to the reproductive phase or the mere elongation of the axis, i.e., "shooting" was inhibited under the subsequent long summer days of May–June with high temperatures of 82° F. to 106° F. and very low relative humidity of 35%. A somewhat similar effect is reported by Sircar and Sen (1951) in Rupsail, a winter rice of Bengal. When this variety is sown on the 25th February flowering has been induced within 62–76 days by 8 hr. short days while the controls flowered after 250 days.

Grain yield. The grain weight has been recorded in the usual manner and is given in Table 3. Statistical analysis of the data is given in Table 4.

TABLE 3. *Grain yield per plant in gms.*
(Average of 24 plants.)

Treatments	Yield in gms.	Percentages of Control
8 hr. S. Day from 1st week till ear emergence	2.28	27.9
8 hr. S. Day from 2nd week till ear emergence	4.24	52.0
10 hr. S. Day from 1st week till ear emergence	3.00	36.8
10 hr. S. Day from 2nd week till ear emergence	4.37	53.6
24 hr. L. Day from 1st week for 20 days	9.98	122.4
24 hr. L. Day from 1st week for 30 days	7.89	96.8
Control	8.15	100.0

S. E. Mean = 0.26; C. D. at 5% = 0.75.

TABLE 4. *Analysis of variance*

Due to	D. F.	S. S.	M. S.	F.	5% F.	1% F.
Between treatments	6	312.16	52.03	126.90**	2.37	3.36
Within treatments	35	14.44	0.41			
Total	41	326.60				

** Significant at 1% level.

Although short-day treatments have brought about considerable earliness in ear emergence there has been no increase in grain yield. As a matter of fact short-day treatments have significantly decreased the yield. The decrease is more where the treatments were started with one week old

seedlings than in those where it started with two week old seedlings. There is no difference between the 8-hour photoperiod and the 10-hour photoperiod so far as their effect on yield is concerned. The 24-hour continuous illumination for 20 days given to one week old seedlings has slightly increased the yield over the controls.

Components of yield. The components of yield such as the number of panicles, length of panicle, total number of spikelets per ear, number of grains per ear and percentage of grains set per ear are presented in Table 5 and their analysis of variance in Table 6.

TABLE 5. *Components of yield*
(Average of 24 plants)

Treatments	No. of panicles	Length of panicle in cm.	No. of spikelets per ear	No. of grains per ear	Percentage of grains set per ear	Weight of 1000 grains in gms.
A. 8 hr. from 1st week	4.00	15.35	86.58	27.71	32.40	20.68
B. 8 hr. from 2nd week	5.54	14.68	87.00	33.10	38.35	23.23
C. 10 hr. from 1st week	4.50	14.26	88.08	31.38	35.90	21.25
D. 10 hr. from 2nd week	6.12	15.08	75.70	32.40	43.15	22.10
E. 24 hr. from 1st week for 20 days	7.75	18.95	108.16	64.11	59.38	20.20
F. 24 hr. from 1st week for 30 days	6.29	17.91	106.05	67.46	63.88	18.78
G. Control	7.33	16.35	97.98	56.21	57.70	19.85
S. E. Mean	0.90	0.82	4.77	1.78	1.80	0.66
C. D. at 5%	2.59	2.38	13.69	5.11	5.17	1.90

TABLE 6. *Analysis of variance of the date of the components of yield*

	Due to	D. F.	S. S.	M. S.	F.	5% F.	1% F.
Characters							
No. of panicles	Betn. treatments	6	68.22	11.37	23.20**	2.37	3.36
	Within treatments	35	17.16	0.49			
Length of panicles	Betn. treatments	6	110.69	18.44	4.46**	2.37	3.36
	Within treatments	35	144.67	4.13			
No. of spikelets per ear	Betn. treatments	6	4,953.04	825.50	6.04**	2.37	3.36
	Within treatments	35	4,782.54	136.64			
No. of grains per ear	Betn. treatments	6	10,677.26	1,779.54	93.56**	2.37	3.36
	Within treatments	35	666.01	19.02			
Percentage of grain set per ear	Betn. treatments	6	5,870.72	978.45	50.25**	2.37	3.36
	Within treatments	35	681.77	19.47			
Weight of 1000 grains	Betn. treatments	6	78.73	13.12	4.98**	2.37	3.36
	Within treatments	35	92.08	2.63			

** Significant at 1% level.

The number of ears per plant is greatly reduced as a result of 8 and 10 hr. photoperiods when given to one week old seedlings. The other treatments have not appreciably altered the number of ears. The length of the

ear has not been affected by either of the treatments. The number of spikelets per ear have been reduced as a result of the short-day treatments of both the durations whereas the long-day treatments have no differential effect. The number of grains per ear, too, have been significantly decreased by the short-day photoperiods. The long-day photoperiod for 20 and 30 days have significantly increased the number of grains per ear in comparison with the control. The percentage of grains set per ear has been reduced in all the short-day treatments, the reduction is more when the treatments were begun with one week old seedlings. The weight of one thousand grains has not shown any decrease as a result of short-day treatments. Rather there is a slight increase when the 8 and 10 hour photoperiods have been given to two week old seedlings.

The chief reasons for the poor yield in the plants receiving short photoperiods are the high reduction of the number of spikelets per ear, number of grains per ear and the percentage of grains set per ear. This reduction is possibly largely due to the excessive heat and the low relative humidity that the plants experienced during the months of May–June under the climatic conditions of Allahabad. While length of day is the primary external factor responsible for flowering, variations in other characters such as yield of grain are chiefly due to the differences in temperature and relative humidity at the time fruit is set and growing to maturity. (Kondo & Okamura 1930, Went 1946, Sircar & Sen 1951.)

Summary

1. Short photoperiods of 8 and 10 hours given to one and two week old seedlings of late sown Dalua (spring) variety of rice grown in Orissa till the time of ear emergence have induced flowering within 3 months as against 7 months required by the control plants.

2. Although the short photoperiod treated plants flowered early, the yield was very poor. There were fewer grains and spikelets per ear. The lower percentage of grain setting observed is attributed to the interaction of high temperature and low relative humidity with the prevailing length of day.

Acknowledgment

Grateful thanks are due to Prof. Shri Ranjan for his guidance and helpful criticism and the facilities provided in the Department of Botany of Allahabad University for carrying out this investigation. I am also grateful to Mr. T. P. Abraham, Statistician, Central Rice Research Institute, Cuttack for his advice in the statistical analyses of the experimental data and to Prof. B. Samantarai, Rovenshaw College, Cuttack, for kindly going through the manuscript and offering suggestions for its improvement.

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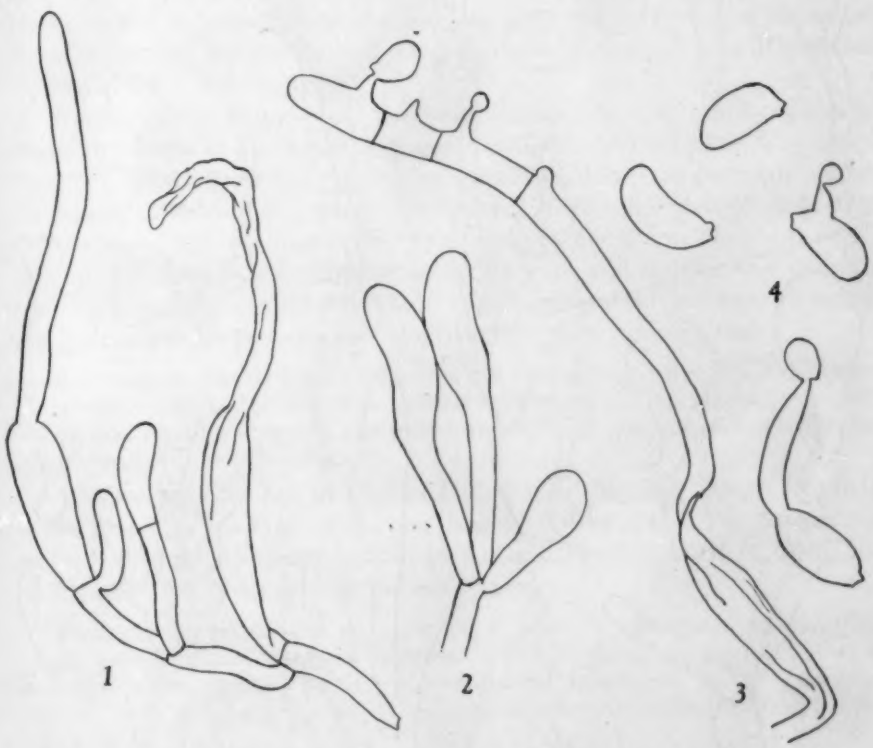
BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 81, No. 4, pp. 329–339 JULY, 1954

NEW OR NOTEWORTHY SPECIES OF TREMELLALES FROM THE SOUTHERN APPALACHIANS—III

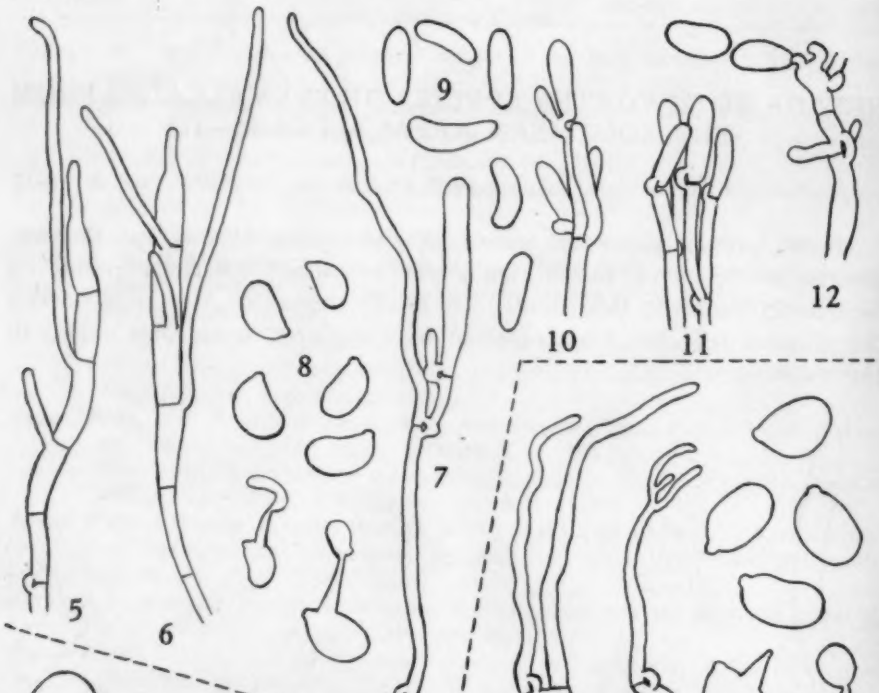
LINDSAY S. OLIVE

In the present paper new species of *Helicogloea, Exidia,* and *Gloeotulasnella* are described. In addition several previously described species not adequately known in this country are briefly discussed. Also included is a list of other jelly fungi not reported from the area in previous papers in this series.



FIGS. 1–4. *Helicogloea terminalis.* Probasidia, basidia, and basidiospores. ×710.

PLATYGLOEA PENIOPHORAE Bourd. & Galz. (Figs. 5–12). This is probably the most variable species in the genus. Although Bourdot and Galzin (1927) list three varieties of it, the present collection does not agree precisely with any one of them. The basidia, which measure 2.7–3.7 × 36–68 μ,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are narrower than in previously described specimens and are often curved and contorted. An empty stalk-like cell may frequently be observed at the base of the basidium, but there is no distinctive, persistent probasidial cell as is commonly found in certain species, including the type of the genus (Olive 1951a). Each basidium produces four long, narrow sterigmata. The basidiospores are more or less allantoid and measure 3.2–5.8 × 6.3–10.7 μ. Conidia are produced abundantly in young fructifications, but are later replaced by the basidial stage. They are formed primarily at the tips of conidial hyphae, and each has a clamp connection at its base while attached to the conidiophore (figs. 10–12). Most of the conidia are somewhat cylindric, and frequently curved. They measure 2.3–4.5 × 7.2–14.4 μ.

The fungus is apparently a parasite. The fructifications of our collection occur as gelatinous pustules which anastomose to form continuous flat layers, pallid to yellowish brown in color, over the surface of a species of *Peniophora*. The fungus was collected on Peace Mountain, near Highlands, North Carolina, July 9, 1953.

When *P. peniophorae* is studied more thoroughly it will undoubtedly be found to consist of a complex of numerous distinctive varieties. The collections previously described by the writer (1946, 1947) as parasitic within the fructifications of *Dacrymyces* lack definite fructifications of their own. Furthermore, the conidia are oval or obovate rather than elongate as in the present collection and as illustrated by Bourdot and Galzin, and they are frequently borne in chains. It would therefore seem advisable to recognize the *Dacrymyces* parasite as a distinct variety of *P. peniophorae*.

PLATYGLOEA PENIOPHORAE var. **interna** var. nov. Nullas fructificationes efformans, ut parasitus internus tantum occurrens in Dacrymycetis fructificationibus. Basidia breviora quam in typo; conidia singulatim vel catinatim producta, ovalia vel obovata.

A collection obtained at Chapel Hill, North Carolina, March 23, 1944, is designated as the type of the new variety (Olive 1946). The fungus was also collected by the writer (1947) in Athens, Georgia, April 11, 1946. The latter collection is designated the paratype.

Helicogloea terminalis sp. nov. (figs. 1–4). Fructificatio tenuis, gelatinosa, pallide grisea. Hyphae enodosae, 2.5–8.1 μ diam.; probasidia plerumque terminalia, erecta clavataque, singula vel aggregata, 10–13 × 43–80 μ; basidia terminalia, 6.6–9 × 63–257 μ; basidiosporae suballantoideae, 5.9–8.6 × 12.6–18 μ.

FIGS. 5-12. *Platygloea peniophorae*. FIGS. 5 and 6. Basidia producing sterigmata. FIG. 7. Probasidium and hypha. FIG. 8. Basidiospores, one producing a secondary spore, another producing a conidium. FIGS. 9–12. Conidia and conidiophores. FIGS. 13–22 *Exidia cystidiata*. FIGS. 13–16. Probasidia and basidia. FIGS. 17–19. Gloeocystidia. FIGS. 20 and 21. Paraphyses. FIG. 22. Basidiospores. FIGS. 23–28. *Tulasnella pruinosa*. Basidia and basidiospores. (All figures × 1065.)

Forming thin, light gray, soft gelatinous patches, up to 7 cm. in length, surface smooth or uneven, occasionally with a whitish bloom. Hyphae without clamp connections, 2.6–8.1 μ broad; probasidia mostly terminal, probably all terminal in origin but occasionally appearing lateral as a result of hyphal proliferation from beneath, erect and clavate, often slightly curved but not constricted, occurring singly or in groups of 2 to 4, measuring 10–13 $\times$ 43–80 μ; basidia arising distally (terminally) from the probasidia, sporogenous portion 4-celled, entire basidia 6.6–9 $\times$ 63–257 μ; basidiospores apiculate, typically somewhat allantoid, 5.9–8.6 $\times$ 12.6–18 μ, germinating by repetition.

Growing on wood and occasionally on bark of birch limb, Highlands, North Carolina, August 14 and 18, 1952.

The new fungus is unique and readily distinguishable from all previously described members of the genus. It is the only species which consistently produces its basidia at the distal ends of upright probasidia. With the exception of *H. intermedia* (Linder) Baker, all the other known species have their basidia produced from the proximal ends of reflexed probasidia. *H. intermedia* has both erect and reflexed probasidia and both types of basidial ontogeny.

The new species is obviously of considerable interest from the standpoint of phylogenetic implications. In general growth habit, texture, and hymenial organization, *H. terminalis* is a typical *Helicogloea*. But its method of basidial development is more like that of *Jola* and of certain species of *Platygloea* which have persistent probasidia. However, *Jola* has small gelatinous fructifications that parasitize mosses, and in *Platygloea* the persistent probasidia, when present, are never so regular in size and shape as they are in *Helicogloea*. Nevertheless, the basic similarities among these resupinate genera are indicative of their close relationship. The existence of such intrmediate species as *H. terminalis* and *H. intermedia* indicate that *Helicogloea* with its characteristic and more specialized saccate probasidia evolved from some other resupinate auriculariaceous form with erect, less specialized probasidia such as *Platygloea* (*pro parte*).

HELICOGLOEA LONGISPORA Baker (Syn. *H. parasitica* Olive.) During the summer of 1953, three collections of a *Helicogloea* occurring in the fructifications of *Sebacina* and *Gloeotulasnella caroliniana* Olive were made in Highlands. These fit the description of *H. parasitica* Olive (1951b), which had been found as a parasite within the fructifications of *Exidia glandulosa*. Also certain striking similarities to *H. longispora* Baker (1946) were noted with respect to microdimensions. The latter had been described as forming mucous-gelatinous fructications on coniferous wood. When the two collections upon which Baker based her diagnosis were re-examined, it was discovered in each case that another jelly fungus was involved, apparently as a host organism. In the type collection the host fungus was in such a deteriorated condition that it could not be readily identified, but it is probably a

Sebacina. In the paratype it is quite clear that the *Helicogloea* spreads through the fructification of a *Sebacina*. In view of the similarities in growth habits and in microscopic characters it is obvious that *H. longispora* and *H. parasitica* are synonymous. The species occurs over a wide range in this country, having been reported in Oregon, Louisiana, and North Carolina.

Exidia cystidiata sp. nov. (figs. 13–22, 52A). Fructificationes gelatinosae, 1–6 mm. lat., libere anastomosantes, massas maiores efformantes gyrosas, albas, vel brunnescentes. Hyphae nodosae; paraphyses tenues, simplices vel ramosae; gloeocystidia aurea vel sature aurantiaco-aurea, clavata, 5.4–12.5 × 22.5–58 μ; basidia stipitato-ovata, quadripartita, 9–13.5 × 16.2–29.7 μ; basidiosporae late allantoideae vel breviter cylindraceae, interdum curvulatae, 6.4–9.1 × 11.3–15 μ.

Fruiting bodies gelatinous, 1–6 mm. in diameter, freely anastomosing and forming larger masses, surface becoming gyrose and sometimes folded, free underneath, whitish to brown, drying to shrunken, resinous-looking bodies. Hyphae with clamp connections, paraphyses simple or branched, slender; gloeocystidia golden yellow to deep orange yellow, typically slender-clavate, often somewhat irregular, 5.4–12.5 × 22.5–58 μ; basidia racket-shaped, mosty 4-celled, 9–13.5 × 16.2–29.7 μ; basidiospores broadly allantoid to short cylindric, often slightly curved, apiculate, 6.4–9.1 × 11.3–15 μ, germinating by repetition.

Growing on decorticate oak limb, Highlands, North Carolina, July 17, 1953 (type) and on dead corticate twigs of *Cornus florida* still attached to tree, September 5, 1953.

Probably the closest relative of this species is *E. alba* (Lloyd) Burt, which has larger fructications and considerably smaller basidia and basidiospores. The basidia of *E. alba* generally lack the stalk-like bases which are characteristic of the new species, and the gloeocystidia of the former are hyaline to light yellow rather than orange-yellow.

Formerly, *Exidia*-like species with gloeocystidia were placed in the genus *Seismosarca*. However, Martin (1951) has given reasons why this generic name is invalid. He accepts Burt's classification of *Exidia alba*, which was formerly placed by Lloyd in the genus *Seismosarca*, and reduces a second species, *S. hydrophora* Cke., to synonymy with *Tremella pululahuana* Pat. The present writer is in agreement with Martin's decision to transfer former species of *Seismosarca* to other existing genera rather than to create a new genus for them. This seems particularly advisable in view of the fact that the various known species fit rather well into several existing genera. The writer takes this opportunity to transfer to the genus *Exidia*, two species recently described by him. The new combinations are as follows: *Seismosarca tomentosa* Olive (1947) = **Exidia tomentosa** (Olive) comb. nov.; *Seismosarca cartilaginea* Olive (1951a) **Exidia fragilis** nom. nov., non *Exidia cartilaginea* Lund & Neuh.

The only other species which has been placed in the genus *Seismosarca* is *S. stratosa* Viegas, which should never have been so classified in the first place. An examination of this resupinate fungus reveals that it has a spongy-coriaceous texture somewhat like that of certain non-gelatinous species of *Sebacina* such as *S. incrustans* and *S. helvelloides*. Its fructifications, however, are thinner and the hymenium contains numerous yellow gloeocystidia. The speices is therefore transferred to the *Bourdotia section* of the genus *Sabacina* as follows: *Seismosarca stratosa* Viegas = **Sebacina stratosa** (Viegas) comb. nov.

Two fine collections of *Exidia fragilis* were recently sent to the writer by F. T. Wolf (1953), who found them in central Tennessee. These are the only specimens of this fungus known outside the type collection.

Guepiniopsis minuta sp. nov. (figs. 49–51, 52B). Fructificationes minutae, 0.8–3 mm. lat., breviter stipitatae vel subsessiles, obscure aurantiacae vel splendide aurantiaco-aureae, pileo pulvinato vel turbinato et superne applanato vel depresso. Hyphae conspicue nodosae; cellulae corticales stricte clavatae vel ample ovales vel obovatae, tunica crassa gelatinosa, 5.4–10.8 × 11.7–38.7 μ. Probasidia matura sublutea, 5–6.3 × 33–50 μ; basidia sterigmatibus duobus praedita; basidiosporae subluteae, cylindraceae, curvulae, denique triseptatae, 4.3–6.7 × 13.5–18.5 μ, germinatione tubulas emittentes vel parva conidia.

Fructifications small, 0.8–3 mm. in diameter, dull orange to bright orange-yellow, firmly gelatinous, cap pulvinate to turbinate and flattened on top, often depressed in center, occasionally irregular, nearly sessile or attached by a short stalk which tapers towards the base, stalk rarely up to 3 mm. long, drying to small reddish orange to orange-brown bodies. Hyphae with distinct clamp connections; cortex covered with narrowly clavate to broadly ovate or obovate cortical cells with gelatinous walls, 5.4–10.8 × 11.7–38.7 μ; mature probasidia yellowish, 5–6.3 × 33–50 μ; basidia 2-sterigmate; basidiospores yellowish, cylindric, slightly curved, becoming 3-septate, 4.3–6.7 × 13.5–18.5 μ, producing germ tubes or small conidia.

On decorticate hemlock log, Highlands, North Carolina, August 18, 1953 (type); on decorticate twigs, along Eastatoe River near Eastatoe, South Carolina, July 25, 1951; on corticate hemlock twigs attached to tree, Highlands, July 22, 1953.

In a recent publication the writer (1953) pointed out that Brasfield (1938) based his description of *Guepiniopsis torta* (Fr.) Pat. primarily on a number of specimens which could not be that species, since the fructifications of these are smaller and the vesicular cortical cells occur singly rather than in chains as in *G. torta*. Most of the specimens identified by Brasfield as *G. torta* and which occur on coniferous wood are probably identical with *G. minuta*. A study of the literature on the Dacrymycetaceae has failed to reveal any species whose description fits the specimens at hand. During the course of this study two collections identified by Lloyd as *G. occidentalis* were obtained for purposes of comparison from the mycological herbarium

of the United States Department of Agriculture, Beltsville, Maryland. This fungus proved to be distinct from ours. Brasfield listed it as a questionable synonym of *G. alpinus* (Tracy & Earle) Brasf., but he must not have examined it, as it is clearly not that species. *G. alpinus* has basidiospores that become 3–4 septate and which measure 5–6 × 15–17.5 μ. The writer finds that *G. occidentalis* has basidiospores that commonly become 7-septate and measure 4.6–6.3 × 7–22.5 μ. The cortical cells are much swollen and have thick gelatinous walls that are externally smooth; they taper apically into blunt beak-like extensions. *G. occidentalis*, therefore, appears to be a distinct species rather closely related to *G. chrysocomus* (Bull.) Brasf., which also has multi-septate but broader basidiospores.

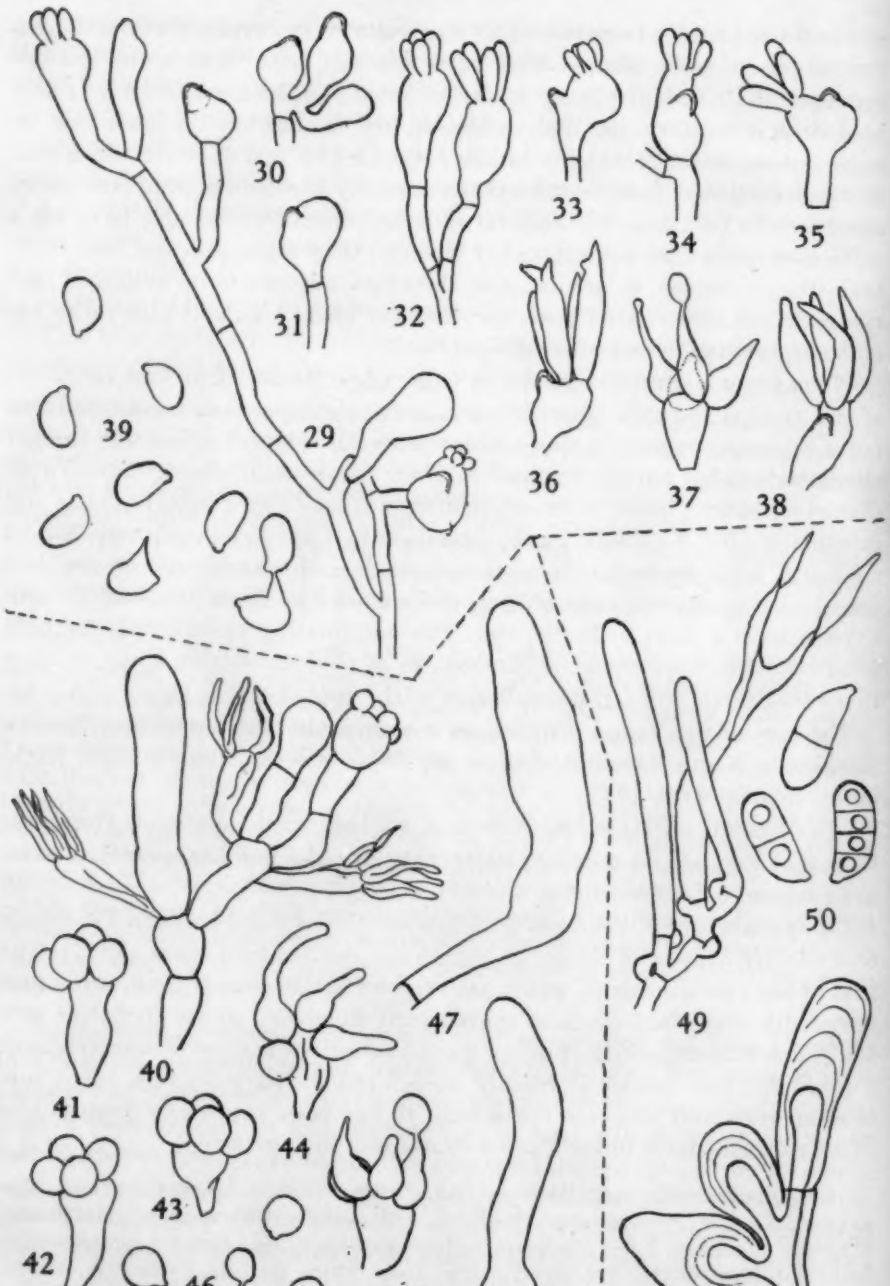
TULASNELLA PRUINOSA Bourd. & Galz. (figs. 23–28). Our first collection of this fungus had thin, grayish to tan, soft-gelatinous to mucous-gelatinous fructifications, very much like a *Gloeotulasnella*. The collection was further characterized by having hyphae without clamp connections, 1.8–5.5 μ in diameter; basidia borne on broad, relatively short-celled vertical hyphae and measuring 4.5–6.3 × 6.3–10.7 μ; epibasidia at first pyriform to clavate, 3.3–4.2 × 6.3–9 μ, later becoming unusually slender as the basidiospores are produced; basidiospores short-oblong, 3–4 × 4.5–6.3 μ. Both the basidia and hyphae have a faint yellowish tint. The germinating epibasidia sometimes produce distinct sporogenous filaments as in *Gloeotulasnella*, while at other times they taper without demarkation to the spore-bearing tip.

The species was found growing on a resupinate thelephoraceous fungus, Highlands, North Carolina, August 20, 1953; also on frondose limb, Highlands, September 8, 1953.

The second collection had very thin, whitish, waxy-gelatinous fructifications that were almost powdery white when dry and basidiospores that measured around 3.2–3.8 × 5–6.3 μ.

It appears that *T. pruinosa* is an intermediate species between *Tulasnella* and *Gleoetulasnella* as those two genera are defined by Rogers (1933). The first of our two specimens, which has very soft-gelatinous fructifications and epibasidia that often produce sporogenous filaments, would fit better into the genus *Gloeotulasnella*, but the second collection is more characteristic of *Tulasnella*. The species is readily recognized by its relatively large subbasidial cells and elongate epibasidia. It has been previously reported in Wisconsin and Iowa in the United States and in Germany.

Gloeotulasnella papillata sp. nov. (figs. 30–39). Fructificationes expansae, tenues, resupinatae, molliter gelatinosae vel mucoso-gelatinosae. Hyphae enodosae, 1.6–4.5 μ diam.; gloeocystidia nulla; basidia clavato-capitata, oblonga, ovata, vel pyriformia, uno latere papilla distincta ornata, 5.9–9.5 × 9–19 μ; epibasidia clavata vel cylindracea, interdum ovata, filamenta distincta sporogena producentia vel ad acumen directe fastigantia,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3.2–5.1 × 7.2–18 μ; basidiosporae ovatae vel breviter cylindraceae, uno latere applanatae vel curvulae, 3.8–4.8 × 6.5–9 μ.

Fructifications thin, extensive, light sordid tan, very soft gelatinous to mucous-gelatinous, nearly invisible when dry. Hyphae 1.6–4.5 μ in diameter, without clamp connections; gloeocystidia absent; basidia clavate-capitate, oblong, ovate or pyriform, frequently irregular or constricted, with or without a stalk-like base, with a distinct papillum or bump on one side, measuring

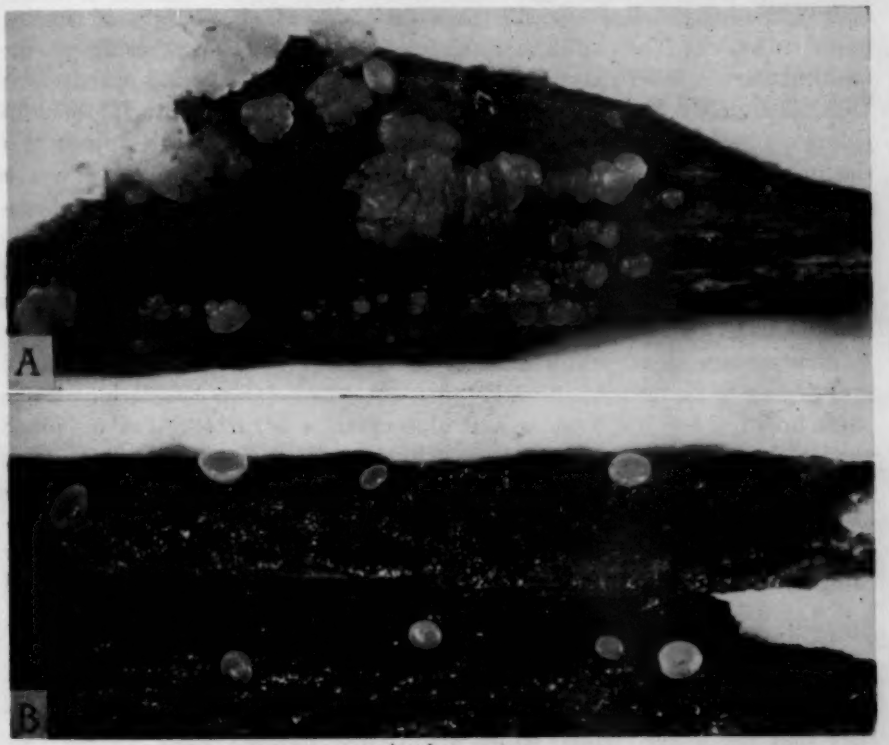

FIG 52. Photographs. FIG. 52A. *Exidia cystidiata*, ×3. FIG. 53B. *Guepiniopsis minuta*, ×3.

5.9–9.5 × 9–19 μ; epibasidia typically clavate or cylindric, sometimes ovate, producing distinct sporogenous filaments or tapering gradually to a point, 3.2–5.1 × 7.2–18 μ; basidiospores ovate to short-cylindric, flattened on one side or slightly curved, apiculate, 3.8–4.8 × 6.5–9 μ, germinating by repetition.

Growing on decorticate oak wood, Highlands, North Carolina, July 17, 1953.

FIGS. 29–39. *Gloeotulasnella papillata*. Stages in the development of basidia, epibasidia and basidiospores. Note papillum with slightly thickened wall on each basidium. FIGS. 40–48. *Gloeotulasnella hyalina*. FIG. 40. Group of basidia and gloeocystidium. FIGS. 41–45. Stages in basidial development. FIG. 46. Basidiospores. FIGS. 47 and 48. Gloeocystidia. FIGS. 49–51. *Guepiniopsis minuta*. FIG. 49. Group of probasidia and old basidium. FIG. 50. Basidiospores. FIG. 51. Cortical cells. (All figures ×1065.)

Like *Tulasnella pruinosa*, the present species has certain features intermediate between *Gloeotulasnella* and *Tulasnella*, as those genera are delimited by Rogers, particularly in the presence or absence of distinct sporogenous filaments on the germinating epibasidia. However, in the absence of any other specimens on which to make a study of variation in the species, it seems that the new fungus fits better into the genus *Gloeotulasnella*. It is clearly distinguished from all other members of the family in having papillate basidia. The papillum, although eccentric in position on the mature basidium, arises as an apical thickening of the wall of the young probasidium (figs. 29 and 30). Since this thickened part is unable to expand further, the enlarging basidium pushes out to one side of it, thus making it appear that the papillum is lateral in origin. The significance of this phenomenon is unknown. The species is further characterized by the production of unusually elongate and slender epibasidia.

GLOEOTULASNELLA HYALINA v. Höhn & Litsch. (figs. 40–48). In view of the fact that this fungus has previously been collected only in Europe and is not adequately known, a description of our collection is included here.

Fructifications very thin and soft gelatinous, nearly hyaline to sordid tan, drying to an invisible film. Hyphae devoid of clamp connections, often quite broad, 2.5–8.1 μ; basidia and gloeocystidia borne together on broad vertical hyphae; gloeocystidia at first hyaline, becoming pale yellow, more or less cylindric, often swollen at the base, 6.7–9 $\times$ 21.6–63 μ; basidia subglobose, cylindric-clavate or clavate-capitate, 6.3–8.6 $\times$ 9–20 μ epibasidia subglobose to ovoid, 4.5–6.3 $\times$ 6.2–7.2 μ, producing very short to considerably elongated sporogenous filaments; basidiospores globose, apiculate, 5–6.8 (–7.4) $\times$ 5.7–7.8(–9) μ, germinating by repetition.

On bark of old oak limb, Highlands, North Carolina, July 17, 1953.

The description of the Highlands collection agrees rather well with previous descriptions of *G. hyalina*, except that there has been no previous report that the gloeocystidia, which are at first hyaline, later become pale yellow.

Other fungi collected in the area but not reported in previous papers (Olive 1951a, 1953) in this series are: *Dacrymyces abietinus* (Pers.) Schröt., *Exidia nucleata* (Schw.) Burt, *Helicogloea lagerheimi* Pat., *Sebacina epigaea* (Berk. & Br.) Rea, *S. deminuta* Bourd., *S. eyrei* Wakef., *S. fugacissima* Bourd & Galz., *S. incrustans* (Fr.) Tul., *S. molybdea* McGuire, *S. sublieacina* Martin, and *Tremella encephala* Pers.

The writer is grateful to Dr. D. P. Rogers for preparing the Latin diagnoses. Type material of the new species has been deposited in the mycological collections of the New York Botanical Garden.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 81, No. 4, pp. 340–352 JULY, 1954

ANNUAL FLUCTUATION IN RATE OF FLOWER PRODUCTION BY NATIVE CYPRIPEDIUMS DURING TWO DECADES[1]

JOHN T. CURTIS

It is a common observation of field botanists that certain years are "good years" for the flowering of various native plant species. The total flower crop in years far exceeds that usually produced by the same species. Other species may have their optima at other times. This annual fluctuation in flower production is particularly noticeable in the native orchids of the temperate zones, and is especially apparent in members of the genus *Cypripedium* L., the temperate zone Ladyslippers. The present study was initiated in 1932 with the aim of describing the magnitude of the annual fluctuation in the various species found in diverse plant communities in Wisconsin. It is part of a long-term series on the ecological life histories of *Cypripedium*, including studies on hybridization, mycorrhizae, seed germination, response to competition, and fruit development (Curtis 1932, 1939, 1943, 1946; Duncan and Curtis 1942).

Acknowledgment is gratefully made to the late Prof. Aldo Leopold and to Dr. H. C. Greene, Dr. Grant Cottam, and my wife, Jane, for aid in making the field counts, and to the late Martin Gillen for generous provision of facilities during part of the study.

Species used. The Cypripediums used in this investigation are listed in Table 1, with nomenclature following that of Fuller (1933). In Wisconsin,

TABLE 1. *Species used in the investigation.*

Cypripedium arietinum R. Br.	Ramshead Ladyslipper
Cypripedium candidum Muhl.	Little White Ladyslipper
Cypripedium parviflorum Salisb.	Little Yellow Ladyslipper
Cypripedium pubescens Willd.	Large Yellow Ladyslipper
Cypripedium reginae Walt.	Showy Ladyslipper
× *Cypripedium andrewsii* Fuller	Andrew's Ladyslipper (hybrid)
× *Cypripedium favilleanum* Curtis	Faville's Ladyslipper (hybrid)

all of these except *C. pubescens* are rather limited in their distribution to certain plant communities or groups of closely related communities. Thus, *C. arietinum*, *C. parviflorum*, and *C. reginae*, are most commonly found in conifer bog forests of *Larix*, *Picea* and *Abies*. *C. candidum* is found in wet prairies of *Andropogon*, *Sorghastrum* and *Calamagrostis*, as are its two hybrids, × *C. Andrewsii* and × *C. Favilleanum*. *C. pubescens* is found abundantly in three types of habitat—wet prairie, oak savanna and forest,

[1] Contribution from the University of Wisconsin Arboretum. Journal Paper No. 27.

and conifer bog forest. As will be shown elsewhere, at least the first two show beginnings of morphological differentiation into recognizable subspecies. All three habitats probably contain distinct ecotypes.

All five species and the two hybrids are similar in general morphology. They produce one or rarely two flowers at the top of an erect leafy stem (the "crown") which arises from a horizontal underground rhizome. All possess, in varying degree, the ability to produce branches from the rhizome and hence to make many-crowned clumps. *C. candidum*, *C. pubescens* and *C. reginae* (and probably the others as well) may fail to send up above-ground crowns in any given year, although the rhizome continues to live and will function normally the following year. In this respect they resemble *C. calceolus* of Europe (Summerhayes 1951). The flower buds are initiated in late summer of the year preceding anthesis. At this time they are still enclosed within a lateral rhizome bud which contains the unelongated internodes and embryonic leaves of the next above-ground crown. Following exposure to the low temperatures of winter, these rhizome buds elongate to produce a leafy crown. There may or may not be a flower at the end of this crown, the absence apparently reflecting unfavorable conditions either at the time of initiation, overwintering, or elongation. If flowers are produced, they remain in receptive condition for 7 to 10 days or more, during which time they may be pollinated by an Andrenine bee or related insect. If pollinated, the ovary will develop into a fruit containing very numerous, extremely minute seeds of characteristic orchid type. The seeds are dispersed by the wind. In the absence of any positive method of inducing germination, no statement can be made as to the average germinability of these seeds, but, to judge from related tropical genera, the potential percentage must approximate 100.

On the basis of field observation and known rates of rhizome growth, it has been estimated that the species here used require from 10 to 16 years between seed germination and plant maturation as shown by flower production (Curtis 1943). This agrees well with the value of 16 years found for *C. calceolus* by Ziegenspeck (1936). Following maturation, the plants are potentially immortal, except for accidental death. Records of plants maintained for more than 20 years under garden conditions were reported by Emerson (1950) for *C. reginae*. As in other perennial herbs, however, the great potential longevity does not result in a steady increase in population numbers at a given site. Rather the population seems to fluctuate about a rather steady mean, indicating that the effective reproductive rate is in equilibrium with the total effect of all decimating influences.

The last statement should perhaps be amended to point out that total populations of all Cypripediums in Wisconsin are actually decreasing and decreasing rapidly. This loss is not due to any defects in the reproductive

capacities of the species but solely to the destructive effect of man on the habitats involved. During the 20 years of this study, over one half of all the stations used have been destroyed completely, and most of the remainder are in serious jeopardy. There is an insistent feeling that the investigations here reported will shortly enter the province of paleoecology.

Methods. The results of the current study were obtained entirely in Wisconsin and adjoining Upper Michigan. Flower production rates determined in other states are omitted for the sake of unity. Native habitats where the plants grew under nearly optimum conditions were used in the study. In addition, certain records of individual plants were obtained for specimens grown under garden conditions at Madison, Wisconsin.

Determinations of flower production were made during the blooming season by counting all crowns which bore one or more flowers and also all mature crowns which were free of recognizable flowers. These two figures were recorded for each separate plant within a station. The determination of maturity in non-flowering plants was a subjective matter, based on long experience, and usually dependent upon size as a criterion. In those species forming large clumps, no serious error was involved, but in the species which usually grew as single crowns it is possible that some called mature were actually immature plants 8–10 years of age. The non-flowering crowns were more difficult to detect in the field than the flowering crowns in the case of the singled crown varieties, even with careful searching. Failure to find all non-flowering crowns resulted in an error in the opposite direction from that caused by mistakes in maturity-judgement.

Determinations of fruit production were made in late summer, by counting fruiting and non-fruiting crowns separately by clumps. In this case, the difficulties of finding all plants were greatly intensified because of the greater height and coverage of the surrounding herbaceous vegetation and the sampling error was correspondingly greater.

The counts of crowns, flowers and fruits were calculated to give figures for crowns per plant, flowering crowns per plant, fruiting crowns per plant, total crown/flowering crown ratios, total crown/fruiting crown ratios and fruit/flower ratios. These figures for each plant were averaged for all plants within a station and for all stations in the same year also for all years for each species. Usual statistical procedures were employed to calculate means, standard deviations, and standard errors. Coefficient of variation, (CV = the standard deviation as a % of the mean) is used as a simple measure of population variability in the presentation of some of the results.

In several instances where very large colonies of certain species were available, a complete tabulation of flowering crowns was made, with the data for each individual plant being recorded separately. From an analysis of these results, it was found that a sample of from 18 to 27 plants

gave a mean which was within 10% of the population mean 19 times out of 20. Accordingly, it was decided to use samples of at least 25 plants at each station. For a few rare species, less than that number were available at one or more stations.

Results. Variation within station within year. The variation in flower production by a population of a single species at a single station in a single year was studied by means of extended series of counts on the individual plants present in a number of large colonies. These counts were combined in various ways, each combination representing a different geographical portion of the area covered by each colony. The counts were also segregated into size classes based on the number of crowns in the individual clumps.

When the values for the different geographical areas were tested for homogeneity by the Chi² method (Snedecor 1940), no evidence of significant place-to-place variation was found in two colonies of *Cypripedium candidum* and one each of *C. pubescens* and *C. reginae,* with probabilities ranging from 0.45 to 0.75. In the case of *C. candidum,* large plants with many crowns per plant are common, while in the other species such large plants are rare. In a large colony of *C. candidum* in the University of Wisconsin Arboretum at Madison, Wisconsin, the flower production of the 10 largest plants was compared with that of the 10 smallest. The large clumps averaged 17.7 crowns per plant, while the small clumps had only 1.5 crowns per plant. The flowering ratio was 0.59 in the large plants and 0.65 in the small plants, but this difference of 0.06 was non-significant by the t-test, with a value of 0.388 compared to the expected 2.878 at the 1% level of significance.

This lack of variation resulting from either clump size or place-to-place location means that the results from a single station in a single year may be relied upon as an index of the reproductive behavior of the given species. The areal homogeneity in flower production is a reflection of the underlying homogeneity of the physical and biotic features of the habitat. Large colonies can be expected to develop only when such habitat homogeneity exists and further, only when the habitat factors are in their optimum range.

Variation between stations within year. It was desired to learn whether the relatively great uniformity of flower production for a given species within one station might extend to other stations within the same general area. For this purpose, the flowering records for *C. pubescens* for six different stations in each of 5 different years were tested for homogeneity by the usual Chi² method. These six stations were located within an area of 36 miles × 60 miles in southern Wisconsin. All were upland forests dominated by species of *Quercus.* No significant deviations from homogeneity were indicated in 4 out of the 5 years, with probabilities varying from .15

to .90. In the fifth year, lack of homogeneity was caused by one station which had a flower production that was much too low in comparison with the other 5 stations. Similar tests with other species revealed about the same range, with significant station-to-station variation infrequent and almost always due to poor flowering in one or two locations. In no case did the majority of stations have low values, with the exceptional station being high. In all of these tests, the stations were within the same general area of not more than 2500 square miles.

These results indicate that a given species reacts about the same to external factors affecting flower production, within the limits of the communities in which it grows. They further indicate that local controls are only rarely effective and that some over-all environmental influence is affecting all plants more or less equally. This regional uniformity permits the data from several stations to be combined into a single average, thereby greatly increasing the validity of that average.

Variation between years. The finding of essential uniformity in flower production within a single station and between stations within a single year leaves year-to-year variation as the only source of the observable flower fluctuations. That such year-to-year variation actually exists is shown by the record of *C. candidum* in a large colony in the University of Wisconsin Arboretum. This colony contained over 4000 plants. Flower production was determined from 1939 to 1952, except for the years 1943 and 1944. The average flower numbers are shown in figure 1, reduced to Fl./Cr. ratios. Also shown are the fiducial limits at the 5% level of significance for each year. As can be seen, there is a pronounced fluctuation in flower production from year to year, with distinct trends shown by succeeding years. In some cases, the values for one year are significantly different from those of the preceding year, as in 1946 and 1947, when the 5% fiducial limits do not overlap. In general, however, any one year does not differ significantly from either the preceding or the following one. The trends are nevertheless obvious and indicate a real change in flower production from year to year.

The variation in fiducial limits in different years shown in figure 1 indicates that the within-station variability is itself subject to fluctuation, with plant response much more uniform in some years than in others. When expressed in terms of comparable units (standard deviation/mean), the coefficients of variation ranged from 18.8% to 55.9%. There was no tendency for the good years of flower production to be accompanied by either very high or very low variations. It must be concluded, therefore, that the factors responsible for annual fluctuation in station averages are not the same as those responsible for plant-to-plant variation within the station.

Annual fluctuation in flower production, as just demonstrated in detail

for a single colony of *C. candidum*, is universally found in all species and hybrids studied. This is shown in Table 2 where flower/crown ratios for all species are given for all years in which records are available. The figures marked with asterisks are based on samples smaller than the preferred size of 25 plants each. This is probably serious only in the case of the two hybrids × *C. andrewsii* and × *C. favilleanum*, where the sample never included more than three plants of each in any one year and in many years was confined to a single plant. The merit of the results with these hybrids is prob-

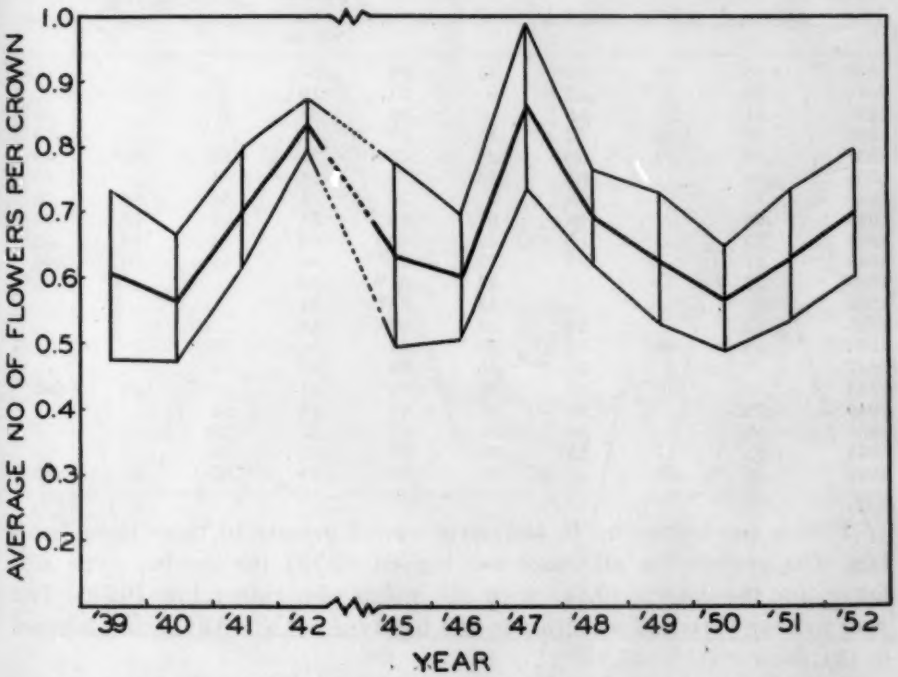

FIG. 1. Annual variation in average number of flowers per crown in *Cypripedium candidum* at one station. The vertical bars indicate the fiducial limits at the 5% level of significance. Note that the years 1943 and 1944 are omitted from the graph.

ably increased by the fact that a single individual plant of each species was followed for each of the 20 years.

The three columns for *C. pubescens* in Table 2 are based on records from three distinct habitat types. That marked oak woods is the common upland oak forest of southern Wisconsin, a rather mesic, lightly shaded community dominated typically by *Quercus alba* and *Quercus rubra* (Curtis and McIntosh 1951). The prairie type is the low prairie (Curtis and Greene 1949), dominated by prairie grasses and typically subject to semihydric conditions in spring. The Cypripediums in the prairie are exposed

to full sun until well past their flowering time when they become overshadowed by later, taller-growing herbs. Both oak and prairie types are found in southern Wisconsin. The bog type is confined to the northeastern half of the state. It is a typical conifer swamp, dominated by *Larix laricina* and *Picea mariana*, with light shade, high moisture content and very acid surface layers of the soil.

TABLE 2. *Average Flower/Crown ratios for all Cypripedium species in all years.*

Year	*andrew.**	*arietin.*	*candid.*	*favill.**	*parvifl.*	*pubesc.* oak woods	*pubesc.* prairie	*pubesc.* bog	reginae
1933	1.00	.66	.35*	.43	.68	.51	.....	.....	.....
1934	.94	.21*	.33	0	.21	.10	.....	.....	.....
1935	.94	.50	.66	.40	.89	.41	.....	.....	.60
1936	.90	1.00	.52	.15	.61	.66	.....	.....	.50
1937	.68	.33	.59	.28	.41	.34	.39	.66*	.46
1938	.94	.....	.55	.23	.71	.54	.54	.....	.76
1939	.90	.....	.58	0	.75	.74	.85	.86	.76
1940	.62	.....	.66	0	.42	.51	.23	.73	.75
1941	.51	.....	.58	.27	.60	.63	.84	.76	.75
1942	.31	.....	.78	.33	.54	.69	.50	.90	.80
1943	.27	.....	.....	.44	.83*	.56	.....	.....	.75*
1944	.27	.....	.....	.44	.86*	.31	.....	.....	.....
1945	.12	.....	.53	.75	.92	.45	.....	.....	.....
1946	.45	.64	.45	.80	.50	.58	.48	.79	.....
1947	.27	.....	.39	.45	.39	.32	.54	.....	.....
1948	.66	.70	.67	.25	.50	.57	.87	.82	.95
1949	.22	.....	.60	.50	.45	.48	.64	.....	.....
1950	.55	.....	.50	1.00	.59	.60	.50	.....	.....
1951	.33	.....	.55	.60	.27	.59	.54	.....	.....
1952	.16	.82	.67	.58	.60	.65	.65	.81	.80

Flower production by *C. pubescens* varied greatly in these three habitats. The average for all years was highest (0.79) for the bog type and lowest for the prairie (0.52) with oak woods also rather low (0.58). The year to year variation was least in the bog type (C.V. 10.9%) and highest in the prairie (C.V. 33.9%).

The annual fluctuation in flower production by all species naturally leads to speculation as to the nature of possible environmental controls. Before exploring the possible correlations between flower behavior and various physical factors such as rainfall or temperature, it is necessary to learn whether the different species reacted the same way in different years. For this purpose, the flower production for each year was graded as high, low, or intermediate, if it was higher than that of the prior and following year, lower than these years, or higher than one and lower than the other, respectively. By means of a Chi^2 two $\times$ two table, it was possible to determine whether the years of high production in any two species were significantly associated, or whether they occurred at random and independently of one another. Any tendency for negative association could also be

determined by this test. In the case of *C. pubescens, C. candidum,* and *C. parviflorum,* there was no indication of any common response. In other words, high production by one species was in no way correlated with either high or low production in either of the other two.

This independence of response is shown very well in the case of the two hybrids, *C. andrewsii* and *C. favilleanum,* for which 20 year performance records of the same plants are available. These plants were grown side by side under garden conditions throughout this period. As can be seen in

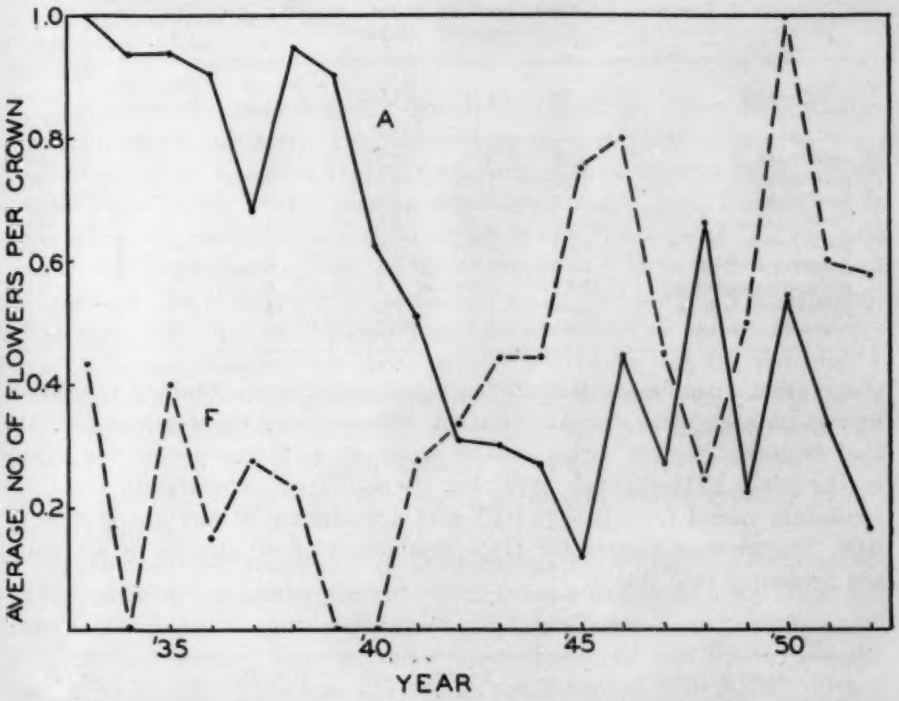

FIG. 2. Annual variation in average number of flowers per crown in one plant each of the two hybrids. (A—*Cyp. andrewsii;* F— *Cyp. favilleanum*), growing side by side under garden conditions.

figure 2, these two plants behaved independently from 1933 to 1939, essentially oppositely until 1945, and then more or less independently until 1952. Any environmental factors which might be correlated with one hybrid would obviously not be correlated with the other. We are faced here with a complex multiple factor response, some of the factors favoring some species at the same time they disfavor others, while other factors may serve to counteract the first under some circumstances and not under others. Such a complicated interrelationship cannot be resolved by correlation of observational data and

only doubtfully would be subject to an experimental approach. It appears, therefore, that little of value would be achieved by comparing flower production with any single factor of the environment or simple combination of these factors. Much longer series of results will be needed before the causal agents can be elucidated. Perhaps the factorial approach recommended by Major (1951) would be of value in this connection.

A summary of average flower production values for all Cypripedium species is given in Table 3, together with numbers of stations and years of

TABLE 3. *Summary of flower production data for all Cypripedium species. (Average of all years)*

Species	Cr./Pl.	Fl./Pl.	Fl./Cr.	No. of Stations	Years of Record	Total No. of Crowns Observed
C. andrewsii	8.88	4.72	0.58	5	20	289
C. arietinum	1.35	1.02	0.64	4	9	77
C. candidum	9.12	5.56	0.60	8	18	12,138
C. favilleanum	10.40	3.50	0.41	4	20	243
C. parviflorum	4.26	2.85	0.59	5	20	1,766
C. pubescens—bog	1.83	1.45	0.81	5	8	354
C. pubescens—prairie	10.89	5.60	0.58	5	13	1,391
C. pubescens—woods	2.96	1.56	0.52	14	20	2,187
C. reginae	7.04	5.29	0.78	4	13	1,288

observation. Insufficient data on fruit production were obtained to present figures on sequential annual variation. Fragmentary observations indicate that fruit production varies at least as much as flower production. Thus in the years 1938 through 1941, the average fruit/crown ratio for *Cyp. candidum* varied from 0.05 to 0.27 with a maximum at any one station of 0.66. The average figures for fruit production of all species in all years are presented in Table 4.

TABLE 4. *Average fruit production.*

Species	Fr./Cr.	Fr./Pl.	Fr./Fl.
Cyp. parviflorum	0.27	0.70	0.49
Cyp. reginae	0.29	1.71	0.23
Cyp. pubescens			
Prairie	0.40	5.33	0.53
Bog	0.57	1.45	0.70
Woods	0.31	0.89	0.42
Cyp. candidum	0.12	1.26	0.22

A few observations on the rate of flower production in native orchids other than Ladyslippers were made as the occasion offered. A summary of these observations is given in Table 5. In most instances, the values for a given year are based on adequate samples, but the number of years of observation is so low as to make the averages tentative only.

TABLE 5. *Flower production in other orchids.*

Species	Ave. Fl./Cr.	No. of Stations	Years of Record
Aplectrum hyemale (Muhl.) Torr.	0.28	2	5
Goodyera pubescens (Willd.) R.Br.	0.33	3	7
Habenaria viridis var. bracteata (Muhl.) A. Gray	0.54	3	6
Habenaria dilatata (Pursh) Hook.	0.40	1	4
Habenaria flava (L.) R.Br.	0.66	1	1
Habenaria hyperborea (L.) R.Br.	0.63	1	1
Habenaria lacera (Mich.) Lodd.	0.62	1	1
Liparis liliifolia (L.) Richard	0.81	3	5
Listera convallarioides (Sw.) Nutt.	0.58	1	1
Orchis spectabilis L.	0.36	7	8

Discussion. The above results demonstrate that the potential reproductive capacity of our native Ladyslippers varies greatly from year to year. Similar behavior has been reported by various investigators for other orchids. Thus Tamm (1948) showed that there was a very highly significant statistical variation in annual flower/crown ratios in *Orchis mascula* and *Orchis sambucina* in Sweden, with a range of 0.14 to 0.78 for the first species and 0.16 to 0.95 for the second in a six year period. The existence of ecotype variation in different plant communities, as shown above for *Cypripedium pubescens,* was demonstrated by Tamm for the non-orchid, *Primula veris.* The average flower/crown ratio was 0.22 (C. V. 52.2%) in a dry meadow, 0.40 (C.V. 19.8%) in a moist *Sesleria* meadow, and 0.69 (C.V. 18.2%) in a woods dominated by *Fraxinus.* Salisbury (1942) also noted variation in reproductive capacity of several species growing in different habitats.

Johnson (1926) reported that fruit production in *Cypripedium acaule* in Connecticut was locally variable, with fruits common in some areas and rare in others, but he gave no figures as to actual rate of production. About 10% of the flowers of *Cypripedium reginae* developed into fruits in Michigan, according to Waterman (1948). In the Eurasian yellow Ladyslipper, *Cypripedium calceolus* L., Detto (1905) reported that 37 fruits were produced by 57 flowers near Jena in 1903. Many records exist of fruit production in those orchid species which produce many flowers on a single spike. Darwin (1877) reported a great range in fruit/flower ratios for various species. Thus *Ophrys aranifera* in Italy produced only one fruit for every 3000 flowers, while related species showed much greater fertility, up to 48 fruits for 49 flowers in *Orchis pyramidalis.* One species, *Ophrys muscifera,* has been studied in detail by a number of workers. Thus Darwin reported a fruit/flower ratio of 0.14 in England, both Müller (1878) and Ziegenspeck (1936) 0.06 in Germany, Detto (1905) 0.02 in 1903 and 0.05 in 1904 in Germany, and Wolff (1950) 0.18 in 1941, 0.11 in 1942, and 0.11 in 1949

in Denmark. Thus both annual variation and place-to-place variation in fruit production appears to be characteristic of the multiflowered orchids as well as the single-flowered Ladyslippers.

The data on flower and fruit production in the Wisconsin study are probably atypical to the extent that the sampling methods required large colonies of each species and such colonies are to be found only in nearly optimum environmental conditions. It is to be expected that flower production would have been lower and much more variable if stations with only a few individuals had been used. It would be of interest to determine whether the reproductive capacity of a species is greater when it is first entering a plant community than when it is being eliminated as a result of successional changes in the community around it (Whitford 1949).

The annual changes in flower production for *Cypripedium pubescens* in the oak woods (Table 2) seem to indicate a 3–4 year cycle in the years from 1933 to 1947 but not thereafter. It is probable that this apparent periodicity is of the same type as that derived from random number tables by Cole (1951). Chance environmental factors, operating independently and at random, may combine to intensify a biological response of a given organism in some years and to decrease it in others. Our present knowledge indicates that such chance factors are responsible for the reproductive variability in the Ladyslippers studied here. If this is really the case, then there is not much point in trying to assess the survival value of the phenomenon, in the manner of Salisbury (1942) and others who postulate that the periodic production of large mast crops in *Fagus* and *Quercus* enables the species to overcome a relatively constant level of predation by squirrels and other rodents. The variation is rather to be thought of as the inevitable consequence of life in a constantly changing environment, with neither positive nor negative value.

There appears to be no connection between the average flower and fruit production of a species and its relative abundance in the vegetation. Thus *Cypripedium arietinum* is by all odds the rarest Ladyslipper species, yet its flower production rate exceeds that of the most common species—*Cypripedium pubescens* in the upland woods. Similarly, the fruit production of *Cypripedium candidum* in the prairie is much lower than that of *Cypripedium pubescens* in the same community, yet the former is very much more abundant. This lack of coincidence between reproductive capacity and biological success of orchids has been noted by many workers (Darwin 1877) and is undoubtedly common in members of other families. Orchids may produce exceedingly great numbers of seeds per plant per year (up to 10,000,000 in certain tropical species), but in spite of this they are typically rare members of the biota. Only in unusual instances does the actual increase in numbers of new individuals approach the po-

tential levels (Curtis and Greene 1953). Much further autecological research will be necessary before complete elucidation of success and the part played in it by reproduction will be forthcoming.

SUMMARY

1. Flower production (in terms of proportions of plants producing flowers) was determined for five species and two hybrids in the genus *Cypripedium* in the period 1933 to 1952. Most of the observations were made in Wisconsin.

2. Plants at a single station and at all stations within a limited geographical area behaved uniformly in any one year.

3. Flower production varied greatly from year to year. The variation was apparently due to chance combinations of random environmental factors. High flower production in one species was not correlated with high production in other species.

4. Fruit production similarly varied from year to year. Fruits per flower ranged from 0.22 in *Cypripedium candidum* to 0.70 in a bog ecotype of *Cypripedium pubescens*.

5. Limited records for other species of orchids, mostly in the genus *Habenaria*, indicated the widespread occurrence of similar variations.

6. No correlations existed between average rate of flower production of a species and the relative abundance of that species in the vegetation.

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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 81, No. 4, pp. 353–362 JULY, 1954

POSSIBLE RELATIONSHIPS AND PHYLOGENY OF SYNCHYTRIUM

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Synchytrium is the most commonly known and largest of the chytrid genera and includes approximately a hundred and fifty species at the present time. These are parasites of algae, mosses, ferns and flowering plants. The genus was established almost a hundred years ago and has been studied extensively throughout the world during this period. However, its relations to other chytrid genera and families and its phylogeny are not clear and certain. In the early years of the genus it was considered to be a connecting link between several groups of simple fungi, but the subsequent discovery of new genera and intensive study of older ones have cast doubt on some of the early concepts of its relationships.

Synchytrium was included first with *Rozella septigena* and *Woronina polycystis* in a sub-family of the Olpidiaceae by Schroeter (1889) on the grounds that the thallus cleaves into segments which become sporangia. Later, Fischer (1892) established a separate family, Merolpidiaceae or Synchytriaceae under the Myxochytridineae for *Synchytrium, Woronina, Rhizomyxa* and *Rozella* with the same basic distinctions used by Schroeter. Thus, *Synchytrium* was associated very early with the family Olpidiaceae and species of *Woronina, Rhizomyxa* and septigenous members of *Rozella,* species which have since been included in the Plasmodiophoraceae or placed temporarily in the doubtful family Woroninaceae because of their biflagellate zoospores. The view that the genus may be closely or distantly related to these three families was accepted with varying degrees of conviction by later writers such as Petersen (1909, 1910), Minden (1911), Gäumann (1926, 1950), Gäumann and Dodge (1928), Gäumann and Wynd (1951), Fitzpatrick (1930), Wettstein (1935), Schussnig (1948), etc. Gäumann, in particular, has stressed the relation of the Synchytriaceae to members of the Olpidiaceae, Plasmodiophoraceae and Olpidiopsidaceae by grouping these families together in the Archimycetes, regardless of the number, relative lengths and position of the flagella on the zoospores.

Considering first the possible relationship between *Synchytrium* and genera of the Olpidiaceae, it may be noted that the structure and behavior of the zoospores are fundamentally similar in both groups. The zoospores are posteriorly uniflagellate with a whip-lash type of flagellum and swim in a similar manner. Also, in some species of *Synchytrium* such as *S. endobioticum* and *S. taraxaci* the resting spore or zygote functions as a sporan-

gium in germination and gives rise directly to zoospores as in species of *Olpidium, Rozella,* etc. Furthermore, sexual reproduction in *Olpidium viciae* and *O. trifolii* is strikingly similar to that of *S. fulgens,* according to Kusano (1912, 1929, 1930b), in that it is isogamous and occurs by fusion of planogametes. In these species the gametes are reported to be facultative. If copulation occurs a zygote develops; if it fails the gametes develop parthenogenetically into gametangia. However, in these *Olpidium* species karyogamy is delayed until shortly before germination of the zygote; whereas in *S. fulgens* it occurs shortly after plasmogamy. Another similarity in life cycle is exhibited occasionally or rarely by *S. endobioticum.* According to Curtis (1921) the sorus of this species occasionally fails to segment into several sporangia and may function in entirety as one sporangium. In such instances the life cycle of *S. endobioticum* individuals may be fundamentally identical to that of *Olpidium viciae* with the exception that a prosorus is not formed in the latter species. Such occurrences, however, appear to be rare and exceptional in *Synchytrium* so far as the genus is known.

Turning to the differences between the two groups, the thallus, sorus or prosorus of *Synchytrium* remains uninucleate until shortly before reproduction begins, whereas in *Olpidium* the nucleus begins to multiply shortly after the thallus enters the host cell, according to Kusano (1912). This difference, however, may not prove to be very important in phylogeny. The most significant difference is the segmentation of the thallus into a sorus of sporangia in *Synchytrium,* whereas in the Olpidiaceae the thallus matures into a single sporangium. Groups of closely adherent sporangia are formed by *Pringsheimella dioica* in the tips of host hyphae, and these may resemble closely the sporangiosori of *Synchytrium* except that they are not surrounded by a soral membrane. Moreover, each sporangium in this species originates from a separate infection and thallus according to Couch (1939).

Division of the thallus into sporangia occurs in the family Septolpidiaceae or Achlyogetonaceae, which has been placed between the Olpidiaceae and Synchytriaceae. *Septolpidium* (Sparrow 1933, 1936, 1942) and *Myiophagus* (Karling 1948) are the fairly well known genera of this family, and at maturity their elongate tubular thalli divide into linear series of sporangia. However, the sporangia are not delimited by progressive cleavage, and they are not surrounded by a common sorus membrane as in *Synchytrium.*

The only other groups of simple fungi in which the thallus cleaves into a sorus of sporangia are the Plasmodiophoraceae and possibly some members of the doubtful family Woroninaceae. Until fairly recently (Karling 1942a) the limits of the Plasmodiophoraceae were not clearly defined, and some of its species were included in the Woroninaceae. Petersen (1909, 1910), for instance, included the families Synchytriaceae and Woroninaceae

in a larger group, the Synchytridineae, indicating thus a fairly close relationship between *Synchytrium* and *Woronina polycystis*, a species which Barrett (1947) has reported to be a member of the Plasmodiophoraceae. In this family, however, the zoospores are anteriorly biflagellate and heterocont, while those of *Synchytrium* are posteriorly uniflagellate. Also, the thallus of the Plasmodiophoraceae is a multinucleate plasmodium, while that of *Synchytrium* consists of a globular cell which does not become multinuceate until shortly before cleavage into sporangia. Furthermore, the zygote of *Synchytrium* develops into a single resting spore, whereas the sporogenous plasmodium of the Plasmodiophoraceae gives rise to a large number of resting spores or cysts which may be united into cystosori in most of the genera. The species of this family, accordingly, may develop both sporangio- and cystosori. Thus, besides the formation of sporangial sori in both groups there is very little similarity in their life cycles. The presence of anteriorly biflagellate heterocont zoospores, plasmodia, schizogony, and the formation of cystosori in members of the Plasmodiophoraceae are the outstanding differences which separate them from *Synchytrium* and preclude close relationship, in the author's opinion. On the basis of present-day knowledge the Plasmodiophoraceae appear to be one of the primitive families of the biflagellate series of fungi, whereas *Syachytrium* belongs in the uniflagellate series. The development of several sporangia from the thallus possibly represents only a parallelism in the development of both groups from different ancestors.

This may be true also with respect to the reported relationships with the so-called Woroninaceae. This family is regarded at present as a dumping ground for a few holocarpic species of *Woronina, Rozellopsis* and *Pyrrhosorus* with biflagellate zoospores (Karling 1942b) which have not been included in the Plasmodiophoraceae or any other family. As such it is not a coherent group of closely related genera, and probably will be discarded as a family when its species are better known. The thallus of these species is reported to be a plasmodium which cleaves into sporangia or spore mother cells, and these give rise to anteriorly or laterally biflagellate, heterocont or isocont zoospores. However, most of the species are only partially known, and it is not certain in some of them whether one or more sporangia are formed from each thallus. In *Rozellopsis* a single resting spore is formed as in *Synchytrium*, while in *Woronina glomerata* the plasmodium gives rise to several resting spores as in the Plasmodiophoraceae. Resting spores are unknown in *Pyrrhosorus*. Accordingly, on the basis of present-day knowledge there does not seem to be any close relationship between these genera and *Synchytrium*.

The family Synchytriaceae includes at present *Endodesmidium, Micromycopsis* and *Synchytrium*, and these genera appear to be fairly closely

related in ontogeny and structure. The species which were formerly included in *Micromyces* are fundamentally similar in life cycle and type of development to *Synchytrium* species, and for this reason they were transferred by the author (1953) to this genus where they constitute the subgenus *Microsynchytrium*. These aquatic species parasitize algae and appear to be closely related to members of *Micromycopsis* and *Endodesmidium* which are aquatic also and parasitize similar hosts. *Micromycopsis* species are very similar to *S.* (*Micromyces*) *zygogonii*, *S.* (*Micromyces*) *longispinosum*, etc. with the exception that their prosori form exit tubes through which the protoplasm passes to the outside of the host cell and develop into epibiotic sori. Occasionally, endobiotic sessile sori like those of *S. zygogonii* are formed in *M. fischeri* also. Accordingly, *Micromycopsis* species may form both epi- and endobiotic sori, but the latter appear to be rare and exceptional.

In *Micromycopsis intermedia*, and probably in *M. mirabilis*, the epibiotic sorus and sporangia give rise to zoospores which swim actively and reinfect the host as in members of *Microsynchytrium*. However, in *Micromycopsis cristata* and *M. fischeri* the discharged zoospores exhibit only jerky and amoeboid movement without becoming actively motile, according to Scherffel (1926) and Canter (1949). They soon lose their posterior flagellum, become quiescent, round up, and their content cleaves into 2 to 6 minute secondary zoospores. Thus, in these two species the first cleavage segments of the sorus are primary sporangia and give rise to primary zoospores which later in turn function as secondary sporangia and form secondary zoospores. In *Micromycopsis zygnaemicola*, on the other hand, the bodies which correspond to the primary zoospores of *M. cristata* and *M. fischeri* do not become motile, but apparently they give rise to zoospores. Accordingly, Cejp (1932) described the first cleavage segments of the epibiotic sorus as sporangiosorus mother-cells instead of sporangia as Scherffel (1926) had done earlier for *M. cristata*. *Micromycopsis zygnaemicola*, however, is not fully known, but present data indicate that the motility of one developmental phase has been suppressed.

In *Endodesmidium* the prosorus gives rise to an endobiotic sessile sorus as in the aquatic species of *Synchytrium*, and as it matures it forms two oppositely directed exit papillae which may or may not pierce the host wall. The sorus content then cleaves into a large number of globular bodies which ooze out singly into the surrounding water or into the cavity of the host cell. These bodies are very sluggish, remaining quiescent or exhibiting only amoeboid movement, and so far no free and active movement has been observed. Only three specimens were found by Canter (1949) with a single posterior thread or flagellum. These bodies become quiescent in a short while and give rise to minute secondary zoospores. Thus, in this genus the

first motile stage is almost entirely suppressed. Furthermore, no cleavage of the sorus into large sporangio-mother cells occurs, and for this reason the entire sorus with its two exit papillae might be regarded as either a single prosporangium or a primary sporangium, depending on whether or not the so-called primary zoospores become motile.

Sporangio-mother cells or pro-sporangia, secondary sporangia and secondary zoospores are unknown in *Synchytrium*, and with the possible exception of *S.* (*Mycromyces*) *ovale* no exit canals have been observed in the genus. These are the principal morphological and developmental differences which separate *Synchytrium* from *Micromycopsis* and *Endodesmidium* species as far as they are known at present.

In postulating relationships and phylogeny within the family on the basis of presence or absence of prosporangia, secondary sporangia and secondary zoospores, *M. cristata* and *M. fischeri* might be regarded as a starting point. From these species suppression of secondary sporangia and secondary zoospores may have occurred along several lines: (1) through *M. intermedia* and *M. mirabilis* to *Microsynchytrium* by way of *S. ovale* which occasionally forms exit canals; (2) through *Endodesmidium formosum* to *Microsynchytrium*, or (3) through *M. zygnaemicola*, in which only one zoospore stage is known, to *Microsynchytrium* as shown in figure 1. In contrast to this supposition Canter regarded *Endodesmidium* as the more primitive of the aquatic genera, and postulated that further suppression may have occurred until it culminated in such species as *S. fulgens* where the sporangial sorus is formed directly from the initial thallus.

At present there does not seem to be much conclusive evidence of an evolutionary series of species within the genus itself, and this may be partly due to the fact that so few species are fully known. However, because of their relative size and similarity to *Micromycopsis* and *Endodesmidium* the members of the subgenus *Microsynchytrium* might be regarded as the most primitive, but this viewpoint depends upon whether or not *Micromycopsis* and *Endodesmidium* are considered to be more primitive. Although resting spores are unknown in these genera it seems that their life cycles are more complex and might be found to embrace more phases of development than *Synchytrium*. In this respect the latter genus may have retrogressed as its species began to parasitize terrestrial plants in the same sense that development of zoospores in some of the Peronosporales appear to have retrogressed in the transition from an aquatic to a terrestrial habitat.

Viewed from this standpoint the subgenus *Microsynchytrium* might be regarded as a link connecting *Micromycopsis* and *Endodesmidium* with the terrestrial species of *Synchytrium*. In members of *Microsynchytrium* secondary sporangia and secondary zoospores are entirely suppressed so far as is known, but their life cycle, nevertheless, appears to be more complex

than that of the most terrestrial *Synchytrium* species in that prosori are present in relation to both the sporangial and resting spore stages. Next in this retrogressing series might be either *Mesochytrium*, or *Eusynchytrium*

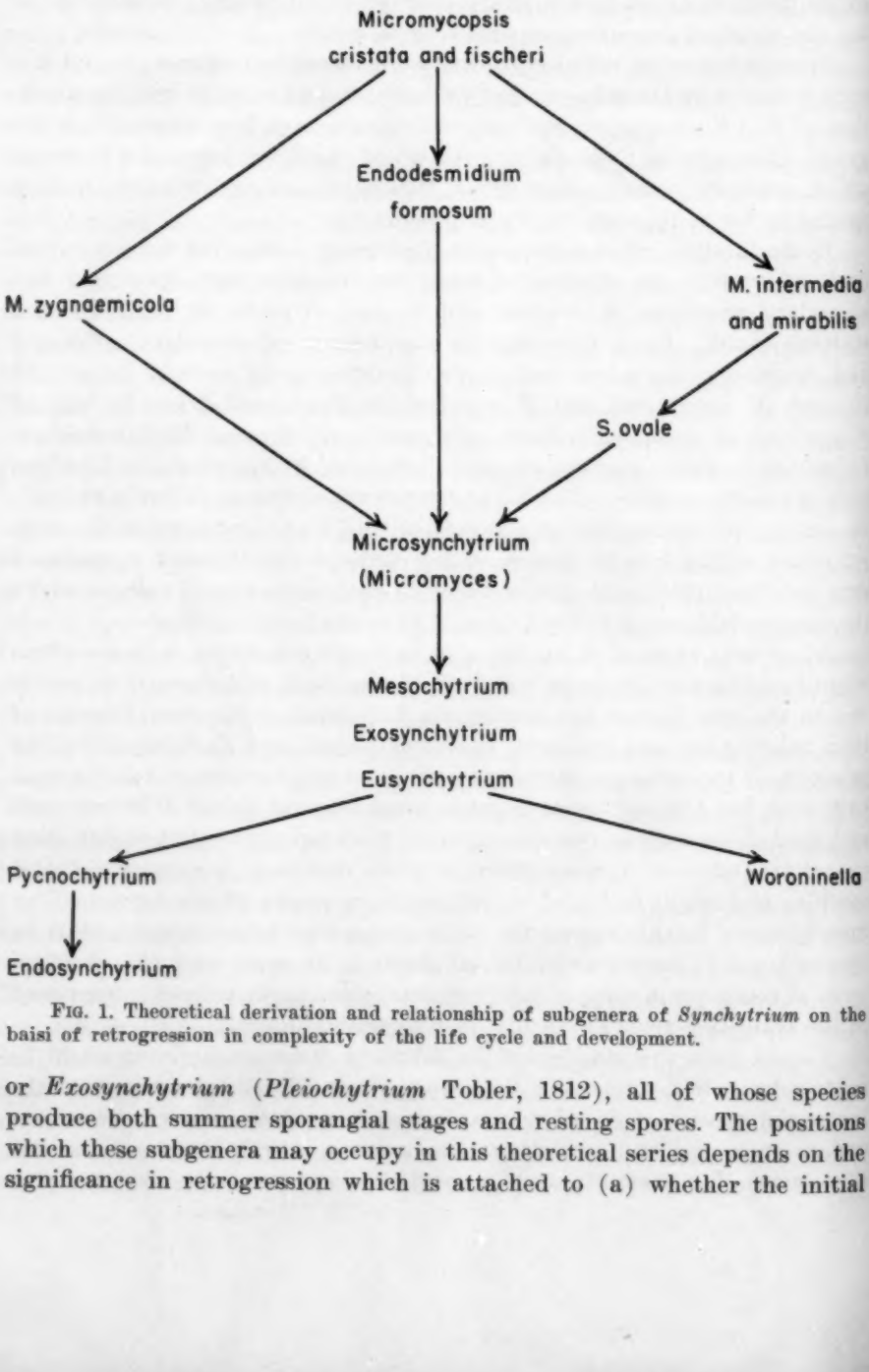

FIG. 1. Theoretical derivation and relationship of subgenera of *Synchytrium* on the baisi of retrogression in complexity of the life cycle and development.

or *Exosynchytrium* (*Pleiochytrium* Tobler, 1812), all of whose species produce both summer sporangial stages and resting spores. The positions which these subgenera may occupy in this theoretical series depends on the significance in retrogression which is attached to (a) whether the initial

thallus functions as a sorus or prosorus, or (b) whether the resting spore functions as a sporangium or prosorus in germination. Possibly, from these subgenera retrogression may have proceeded in two directions: (1) to *Woroninella* in which resting spores are lacking or unknown, and (2) to *Pycnochytrium* and *Endosynchytrium* in which apparently summer sporangial sori or prosori are not developed. *Endosynchytrium* might be considered as the most retrogressed subgenus known inasmuch as the resting spore functions as a sorus in germination. To carry this hypothesis further, it is not altogether improbable that *Synchytrium* species might be found whose entire life cycle consists of either a resting spore which functions as a sporangium and gives rise to zoospores directly in germination, or a summer thallus which functions in entirety as a sporangium. Such species would represent further regressions from *Endosynchytrium* and *Woroninella*, respectively, and be almost identical to some species of *Olpidium*.

It is just as probable, on the other hand, that *Woroninella* and *Endosynchytrium* might be the most primitive subgenera, and through them have evolved the more complex species of *Synchytrium*. Obviously, either view is largely theoretical and based on present-day incomplete knowledge. Without minimizing Canter's excellent studies, the author believes that much still remains to be known about the aquatic Synchytriaceae, and as emphasized frequently elsewhere (Karling 1953, 1954) less than a fifth of the terrestrial *Synchytrium* species are fully known. As these become better known and new aquatic genera and species are discovered the above concept of the relationships and phylogeny of the genus may prove to be entirely wrong. However, for the time being it may prove to be valuable and stimulating as a working hypothesis.

Kusano (1930a and b) proposed a theory of retrogression which is based on sexual reproduction, and assumes that the motile cells of *Synchytrium* are either obligatory parthenospores, or facultative, or obligatory gametes. He assumed that the resting spore of *Pycnochytrium* is formed as the result of gametic fusion, and since no summer sporangial sori occur in this subgenus he regarded its motile cells as obligatory gametes which are incapable of parthenogenetic development into sporangial sori. Accordingly, he regarded this subgenus or those species which possess obligatory gametes as the original or most primitive. From this group retrogression proceeded to species like *S. endobioticum* and *S. fulgens* (*Mesochytrium* and *Exosynchytrium*, respectively) in which the gametes are facultative, (capable of either fusion or parthenogenetic development) and finally to species (*Woroninella*) whose gametes have lost their sexual property and become obligatory parthenospores. On the other hand, the opposite view is equally plausible, as Kusano pointed out. The sexless species may be the primitive members, and from them evolution progressed through the species with faculta-

tive gametes to those with obligatory gametes. However, both of these theories are based on the assumption that the resting spores of *Pycnochytrium* are formed by fusion of obligatory gametes, which has not been proven.

From the standpoint of nuclear division Pavillard (1910) and Bally (1911, 1913) believed that *Synchytrium* shows affinities with the Sporozoa. Bally, who believed that amitosis occurs in *Synchytrium,* emphasized its similarity to that which is reported to occur in the Coccidiae, and maintained that the process of heterochizis described by Griggs (1908, 1909a, b and c) in *Synchytrium* is analogous to the divisions of the polyenergic nuclei in *Adelia ovata.* He also believed that nuclear budding and chromidial extrusion in *Synchytrium* is the same as occurs in *Eimeria schubergi.* In light of Rytz's (1917) and Kusano's (1930a) studies showing that heterochizis and nuclear budding may be abnormal and pathological and that mitosis is the regular method of nuclear multiplication in *Synchytrium* the cytological analogies cited by Bally do not seem significant from the standpoints of relationships and phylogeny.

In this connection it may be noted that the unusually large size and structure of the primary nucleus in *Synchytrium* are similar to those of the nucleus of the parasitic alga *Rhodochytrium* (Griggs 1912). Furthermore, the primary nucleus of this alga does not divide until shortly before reproduction as in *Synchytrium.* Because of these cytological similarities Griggs believed that *Synchytrium* might have been derived from a proto- or chlorococcoid ancestor, a viewpoint which had been expressed earlier by Cohn (1872). Although such algal species are parasitic in higher plants and resemble superficially *Synchytrium,* they produce anteriorly biflagellate zoospores or gametes. This difference together with the fact that their thalli do not segment into a sorus of sporangia indicates that they have little in common with *Synchytrium.*

SUMMARY

1. The relationships and phylogeny of *Synchytrium* are not certain. The aquatic species, which were formerly included in *Micromyces* and now constitute the subgenus *Microsynchytrium,* however, show close affinity with *Micromycopsis* and *Endodesmidium,* two aquatic genera of the family Synchytriaceae.

2. In postulating relationships and phylogeny within the family on the basis of presence or absence of prosporangia, secondary sporangia and secondary zoospores, *Micromycopsis cristata* and *M. fischeri* might be regarded as primitive.

3. From these species suppression of secondary sporangia and secondary zoospores may have occurred along several lines: (1) through *M. intermedia* and *M. mirabilis* to the subgenus *Microsynchytrium* by way of *Syn-*

chytrium ovale which occasionally forms exit canals; (2) through *Endodesmidium formosum* to *Microsynchytrium;* or (3) through *Micromycopsis zygnaemicola,* in which only one zoospore stage is known, to *Microsynchytrium.*

4. The subgenus *Microsynchytrium* might be regarded as a link connecting *Micromycopsis* and *Endodesmidium* with the terrestrial species of *Synchytrium,* which may possibly have retrogressed in complexity of life cycle as they began to parasitize land plants.

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BULLETIN OF THE TORREY BOTANICAL CLUB

VOL. 81, NO. 4, PP. 363–370 JULY, 1954

TORREYA

NEW STATIONS FOR HABENARIA INTEGRA IN BURLINGTON COUNTY, N. J.

DAVID FABLES

The Southern Yellow Orchis, *Habenaria integra*, (Nutt.) Spreng. was discovered by Thomas Nuttall in 1818 at "Egg Harbour" in Atlantic County, N. J. This would be Beesley's Point on present-day maps. As knowledge of the range of the species increased, it became apparent that this and other New Jersey stations located later were disjunct ones. According to Correll, (1950) *Habenaria integra* ranges over the Coastal Plain from New Jersey to Texas, occurring also in the Piedmont and mountains of North Carolina, and on the Cumberland Plateau in Tennessee.

In New Jersey it was next found at Quaker Bridge in Burlington County by Charles Pickering, and on August 26, 1863 was collected there by Charles F. Parker. Dr. P. D. Kneiskern lists it in his "Catalogue of Plants . . . of Monmouth and Ocean Counties," but Witmer Stone expressed the opinion that an error may have been made as Kneiskern does not report *Blephariglottis* (*Habenaria*) *cristata* from his area though the latter plant is well known from this region. The same may be true of Rev. Samuel Lockwood's report of the species to Dr. N. L. Britton from Allaire. Apparently neither of these reports is substantiated by specimens. The species was relocated by George Reddles at Quaker Bridge around 1900, though no specimen was preserved. At the conclusion of his work "The Plants of Southern New Jersey" (1910), Stone was forced to admit: "All our efforts to find this orchid have failed, although likely spots in the Pine Barrens have been diligently searched." Shortly after the publication of Stone's monumental flora, the species came to light on the Cape May peninsula.

On August 16, 1912, Dr. Henry Fox (1913) found two plants of it along the railroad near the village of Swain. This locality was visited two years later by a party of members of the Wild Flower Preservation Society from Washington, D. C., and 5 or 6 additional plants were observed. Morris and Eames (1929) studied it there.

The plant was next found in a savanna at Sym Place near Warren Grove, Burlington County. Vernon L. Frazee, discoverer of the station, came upon it quite by accident as he wandered over poor roads near the Plains around 1932. This to date remains the largest known station in the State, over two-hundred plants blooming in most years. The plants have bloomed equally well in dry seasons and in wet ones.

No additional stations for *Habenaria integra* were located during the next nineteen years.

While engaged in making a plant survey of Penn State Forest in Burlington County, the writer chanced upon three plants of *H. integra* in an open bog bordering Breeches Branch of the Oswego River, about one-half mile upstream from Lake Oswego. This was August 17, 1951. A return visit on August 24, 1951 revealed that one plant had been uprooted and another had been chewed at the top. The third plant was still intact. Many tracks in the vicinity indicated that the White-tailed Deer (*Dama virginiana*) probably had feasted upon the orchids. It is possible that other stations are decimated in similar fashion. In this same bog grew several plants of *Tofieldia racemosa* and hundreds of *Narthecium americanum*, as well as numerous specimens of *Pogonia ophioglossoides* and *Calopogon pulchellus*.

The 1952 season was an extremely wet one in the Pine Barrens, and the water table remained high throughout the summer. Several visits to the now inundated bog along Breeches Branch revealed no *H. integra*, *Tofieldia*, or *Narthecium*. There were a few *Pogonias* and *Calopogons*. Although the 1953 season was dry, no plants of *H. integra*, *Tofieldia* or *Narthecium* revealed themselves in the bog.

Meanwhile, during the 1952 season, Frank Hirst and Robert Leisy spent considerable time in the vicinity of Quaker Bridge searching for Parker's station. On July 22

they located plants that looked "different" in the bud stage from *H. ciliaris*, *H. blephariglottis* or *H. cristata*. The latter two species were in full bloom nearby. A return visit on August 16 revealed sixteen plants of *H. integra* in flower. This station is in a bog along the Batsto River upstream from Quaker Bridge. Over thirty members of the Torrey Club saw the flowers, August 9, 1953.

On September 6, 1953, the writer, in company with Messrs. Hirst and Leisy, found one *H. integra* in bloom in a savanna on the Atsion River, downstream from the road from Atsion to Quaker Bridge, and on the eastern side of the river. Later the same day a score or more plants were located (one in full bloom) in a savanna on the western side of the Batsto River, also downstream from the road from Atsion to Quaker Bridge.

Plant associates in bloom at this season in all of the stations along the Batsto and Atsion Rivers include: *Rhynchospora cephalantha*, *R. oligantha*, *R. gracilenta*, *Xyris fimbriata*, *Juncus caesariensis*, *Spiranthes praecox* and *Lobelia canbyi*. Previous to these discoveries, *R. oligantha* had been reported in New Jersey only from the vicinity of Chatsworth, Speedwell and Washington along the Wading River.

Apparently the bogs, savannas and cedar swamps along the Batsto and Atsion Rivers harbor quite a few stations for species hitherto recorded at only one locality or two in the State. *H. integra* doubtless will be found in other savannas in the region. —Biology Department, Union Junior College, Cranford, N. J.

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LOWLAND LYCOPODIUMS IN THE NEW JERSEY HIGHLANDS

Four miles northeast of Culvers Gap, Sussex County, New Jersey, there is a small lake designated on the topographic map Skellinger, but now known as Wapalanne. The state maintains a conservation school nearby and the native plants are largely undisturbed in the vicinity. During a visit there on September 12, 1953, small peaty areas on the lake shore were observed to support colonies of bog clubmosses. The only one of these to be expected in this glaciated territory at 750 feet altitude was *Lycopodium inundatum*, and this indeed proved to be fairly abundant. Surprising, however, was the finding of one small but luxuriant colony each of *L. adpressum* and *L. alopecuroides*. The carefully compiled range-maps in Chrysler and Edwards' Ferns of New Jersey (1947) show no previous collections of these to have been made northwest of a line connecting northeasternmost Somerset and eastern Bergen counties, so a considerable range extension is represented by these finds. Specimens are being placed in the herbarium of the Academy of Natural Sciences of Philadelphia.—EDGAR T. WHERRY.

NOTES ON RECENT BOTANICAL LITERATURE[1]

H. W. RICKETT

In recent years C. W. Wardlaw has made a notable series of experiments, including skillful dissections and surgery, on shoot apices. (Such work straddles the line between

[1] See Bull. Torrey Club 81: 251–253. 1954.

morphology and physiology, for which reason it is not surprising that it is reviewed in Ann. Rev. Pl. Physiol. 2: 269–292.) He now reports a study (Ann. Bot. II. 17: 513–527. *pl. 27–30*) of the formation and development of buds in *Ophioglossum vulgatum* from both shoots and roots; in roots they are said to develop either from the apical meristem or endogenously from the cortex. F. A. L. Clowes has recently applied similar techniques to investigations of the root tip (New Phytol. 52: 48–57. 53: 108–116); he has now studied grass roots as well as those of beans and beech. He is led to postulate a "cyto-generative centre," a cup-shaped promeristem, from which the initials of the various tissues are formed; the histogen theory in modified form. After various types of incision through or near the apex, missing parts are regenerated but differ in the radial arrangement of the cells; in the absence of a subapical promeristem, removal of the apical region would, he says, have prevented any regeneration—which it did not; and if an uninjured part of the apex had regenerated the new cells, their arrangement would not have been disturbed.

Chimeras in stem apices, consisting of layers of cells differing in chromosome number ("ploidy"), have been much used in studying the origins of tissues. Haig Dermen has reported a peach chimera of this kind, in which the chromosomal content of the cells of the meristem was determined from cell and nuclear size and from smear preparations (Am. Jour. Bot. 40: 154–168). He concludes that the epidermis of stems and leaves arose only from the outer cell-layer of the apex, and the mesophyll and vascular tissue aside from the midrib only from the second layer; but the third layer contributed to a varying extent to the petiole and midrib, so that there is no exact relationship between apical layers and the mature vascular system. Likewise the second layer contributed to the cortex of the stem to a varying degree; sometimes even to the stele. He used the same method to investigate the old question of the homology of the apple (Jour. Hered. 44: 30–39). The meristem was "2-2-4," i.e. the two outer layers were diploid, the third tetraploid. The fruit had irregular patches of tetraploid tissue mixed with diploid, and so is concluded to be "appendicular"; if it had been "axial" it should, he says, have been all tetraploid. However, Dermen makes it clear that the fruit is not made of parts that "fuse" in ontogeny; it is one from the beginning; in the light of his discussion the controversy seems rather meaningless. Sanford D. Tepfer provides a study of floral structure and development in *Aquilegia* and *Ranunculus*, embellished by beautiful photographs of dissected apices and of sectioned material (Univ. Calif. Publ. Bot. 25: 513–648. *pl. 47–81*). Contrary to the contention of Grégoire, the floral shoot is not different in structure from the vegetative, the transition in mode of development being gradual. He has an illuminating discussion of "homology," in the light of which attempts to label floral parts "appendicular" or "axial" seem merely verbal exercises.

R. H. Wetmore and his associates have published several papers on experimental studies of abscission of leaves. The blade apparently retards[2] abscission through the auxin which diffuses from it into the petiole; this effect may be duplicated by the application of IAA or NAA in lanolin to the stumps of debladed petioles (Wetmore & Jacobs, Am. Jour. Bot. 40: 272–276). But Rossetter and Jacobs have shown also that leaf-blades *accelerate* abscission of *nearby* petioles (Am. Jour. Bot. 40: 276–280); the stimulus is not auxin, but is perhaps ethylene. Jacobs and Bullwinkel showed that excision of buds and branches results in a longer stem bearing larger leaves which unfold more rapidly; and that this is not connected with competition for auxin (Am. Jour. Bot. 40: 385–392).

Everyone knows of the use of growth rings in studying the history of wood; some know also of the unreliability of the method. Duff and Nolan (Canad. Jour. Bot. 31: 471–513) have analyzed growth rings in pine not only at one level but from tip to base, and have demonstrated an intrinsic "pattern" in the width of the rings. They show that the width of a ring depends on its position in the stem as well as on extrinsic factors; it is greatest in the 3-year-old internode. Variation in internodal length is dependent on extrinsic factors and is correlated with width of rings in a rather complex manner.

[2] The use of the word "inhibits" for this effect is perhaps unfortunate.

Arthur J. Eames describes the ontogeny of the palm leaf—a strangely neglected subject (Phytomorphology 3: 172–189). In this family the pinnate type is more primitive than the palmate; but the pinnae are formed in an entirely different manner from those of other groups. The plicate structure appears when the primordium of the leaf is only about 1 mm. long; the pinnae are torn apart by the elongation of the rhachis; the "reins" are formed from the detached margins of the leaf. The ontogeny affords evidence for the phyllode theory of the monocot leaf. B. J. de Laubenfels classifies conifer leaves into four types by external morphology (Phytomorphology 3: 1–20); the ancestral type, he concludes, was spirally arranged, amphistomatic, pointed, serrate, tetragonal in cross section. The broad flat type is the most advanced.

Many morphological studies are really taxonomic—they are concerned with the relationships of groups of plants. Vernon I. Cheadle demonstrates that vessels have originated independently in monocots and dicots (Phytomorphology 3: 23–44); monocots have vessels first in their roots, and must have developed from woody dicots, many of which lack vessels. Bahadur Singh concludes from a study of the seeds of Cucurbitaceae (Phytomorphology 3: 224–239) that this family is not allied to other Sympetalae. The origin of the seed habit from heterosporous ancestors is questioned by J. Doyle (Ann. Bot. II. 17: 465–476) on the basis of measurements of micro- and megaspores (principally in conifers); the latter are no larger than the former and often smaller. This involves the question of what to consider the spore—the structure immediately derived from meiosis, or the entire gametophytic ontogeny. The terms gynospore and androspore are suggested. Chester A. Arnold discusses the origin and relationships of the cycads (Phytomorphology 3: 51–65), and finds no discernible relation with the coniferophytes.[3]

Cormack and Gorham show that sun and shade leaves are not preformed in the season before they open; their structure is influenced by the conditions under which they unfold (Canad. Jour. Bot. 31: 537–541). They used *Menziesia glabella* and *Lonicera glaucescens*. Scott and Lewis describe the occurrence of pits in the walls of meristematic cells of several species and the presence of a "pellicle" of suberin lining the intercellular spaces (Bot. Gaz. 114: 253–264); features which disturb our usual concept of meristem. Else and Olaf Hagerup studied the pollination of *Erica tetralix* (New Phytol. 52: 1–7) and show that many insect visitors are not able to effect transfer of pollen; this is accomplished by winged female thrips, which fly from flower to flower "in order to find" the wingless males (how they have previous knowledge of the existence of their future partners is not revealed).

David W. Bierhorst obtained gametophytes of *Psilotum* from greenhouse soil and presents a careful description of them (Am. Jour. Bot. 40: 649–658). The versatile E. J. H. Corner of Cambridge University has a paper on the structure of polypores (Phytomorphology 3: 152–167), describing skeletal, binding, and generative hyphae and monomitic, dimitic, and trimitic types of construction. He thinks that the group is polyphyletic. Corner was the author of the "durian theory" of the evolution of angiosperms, which now receives somewhat adverse criticism by John Parkin (Phytomorphology 3: 80–90). Sexuality in the myxomycete *Dictyostelium* was first reported by Skupienski in 1920, and generally disbelieved. Now Charles W. Wilson gives us the first account of meiosis in the Acrasiales and confirms the occurrence of syngamy—of an unusual type (Am. Jour. Bot. 40: 714–718). Mating in *Saccharomyces* also is described by M. Ahmad (Ann. Bot. II. 17: 329–342), and the life-cycle illustrated.

The flagella of *Chlamydomonas* are beautifully represented in electron-micrographs in a paper by Lewis and Meinhard (Canad. Jour. Bot. 33: 711–717. *pl. 1–3*). Each flagellum is composed of 9–11 fibrils in a hollow cylinder, embedded in less solid material. The electron microscope was used also by Steward and Mühlethaler in a study of the cell wall in Valoniaceae (Ann. Bot. II. 17: 255–316. *pl. 9–17*). The first wall is described as a "tangle of fibrils" in a homogeneous matrix. Later layers are formed of

[3] I cannot forbear commenting on the extraordinary grammatical misuse of family names by many botanists: "The Cycadaceae is . . ." The name of a family, as the *International Code* says, is a plural adjective used as a substantive. The quoted phrase is exactly equivalent to "the cycads is. . . ."

parallel fibrils, their direction changing by 120° in successive lamellae. Since enlargement of the cell and deposition of the wall are concurrent, the lamellae are torn and the fibrils become irregularly separated.

The history of science would not lead us to look to Asia for new developments in botany or even for the facilities of publication; yet PHYTOMORPHOLOGY, edited at Delhi and printed at Ranji, is now in its fourth year, and, as many of the above references indicate, is a valuable avenue of publication for morphologists all over the world. The editor, Panchanan Maheshwari, is known for his studies on the embryology of angiosperms; and an impressive series of contributions on this subject, mostly by Indian botanists, is to be found in this periodical.—The New York Botanical Garden

BOOK REVIEWS

Manual of North American Smut Fungi. By George William Fischer. xii + 343 pp. 136 figures. The Ronald Press Co., New York. 1953. Price $8.75.

The smuts constitute one of the two most important taxonomic groups of fungi from the standpoint of damage done to major crop plants, rivalled only by the much larger group of rusts in this respect. It is, therefore, fortunate that a complete and modern descriptive treatment of the North American species is now available. In the work under consideration, 22 genera, 276 species and some varieties occurring on 242 host genera are recognized; each is described, the hosts listed and the distribution noted and the great majority are illustrated. The basis for classification is mainly morphological, although in some cases morphologically identical forms occurring on hosts belonging to different families are treated as specifically distinct. The classic arrangement into two families based on spore germination is disregarded as impractical. A key to genera which ignores this distinction represents an enlargement of Clinton's old but extremely useful key of 1904. The key which will be used most, however, is based on the host genera. These are listed in alphabetical order by genus, and, if there are two or more smut species occurring on a genus, they are keyed out under the host genus. The smuts are arranged alphabetically by genera, and by species within each genus. This is a great convenience for those who consult the book and while there is a complete index, the latter will have to be consulted much less often than is the rule in books of this sort.

The illustrations are helpful. Some of the photomicrographs of spores and spore aggregations are less sharp than might be desired, but when examined in the light of the accompanying text are always helpful; many of them are excellent.

In a foot-note on p. 9, the author defends the use of the terms "smut spore" or "spore" rather than "teliospore" or "chlamydospore." The last named has little justification in this connection; "spore" is rather vague. "Smut spore" is certainly sufficiently precise and involves no theoretical decisions. It will still seem to many that the evidence points very strongly to the homology of the smut spore with the rust teliospore, or rather, teliospore cell, and that the terminology should eventually reflect this in some way or other.

In addition to its completeness, the most noteworthy feature of the book is its eminent practicality, given accurate determination of the host. It will be of great service in mycological and plant pathological laboratories, not only in North America, but elsewhere, since many of the hosts are grown or occur naturally over wide and extra-limital areas.—G. W. MARTIN, University of Iowa

A Preliminary Checklist of Jamaican Pteridophytes. By George R. Proctor. 89 pages, 3 plates. Bulletin of the Institute of Jamaica, Kingston, Jamaica, B.W.I. May 1953. 6 shillings.

Although ferns and "fern allies" have been collected in Jamaica for 250 years, literature helpful to a botanist visiting the island is distinctly unsatisfactory. The present administration of the Institute of Jamaica has taken steps to correct this situation, and the checklist is to be regarded as a step in the direction of a work which will realize the

late Dr. Maxon's plans for a manual of the fern flora. Much field work has been accomplished by Proctor, who has collected in every Parish, including an unexplored "elfin forest" in the John Crow Mountains (Parish of Portland), where he has discovered two new species of *Grammitis* and one of *Trichomanes*, all of which are duly described and figured.

The systematic part of the bulletin recognizes 524 species, with the range indicated by a list of the Parishes in which each species has been collected, and in many cases with further exact data. The dryopteroid ferns are placed in three genera: *Ctenitis, Dryopteris,* and *Thelypteris. Alsophila, Cyathea* and *Hemitelia* are "for the present" merged under *Cyathaea. Diplazium* is retained, likewise *Gleichenia.*

Jamaica has been considered a centre of endemism, but the author points out that with respect to Pteridophytes the number of endemics is not more than 14%; the sheet of *errata* lists 17 species which have recently been found also in *Hispaniola.* This would reduce the endemic species of Jamaica to less than 11%.

The formal systematic portion of the bulletin is followed by a seventeen page "Discussion of the Parishes"—what might be called a phytogeographic sketch, which the general reader will find of much interest.—M. A. CHRYSLER, Rutgers University.

Plant Genera: their Nature and Definition. A Symposium by G. H. M. Lawrence, I. W. Bailey, Arthur J. Eames, Reed C. Rollins, Marion S. Cave, and Herbert L. Mason. Chronica Botanica **14**: 83–160. 1953. $2.00.

A "symposium" was originally a drinking-party: "a convivial meeting for drinking, conversation, and intellectual entertainment" (OED). The eminent botanists who made up the symposium on plant genera, however, seem not to have conceived their function in these terms; we must substitute a derived meaning: "a meeting or conference for discussion of some subject; hence, a collection of opinions delivered, or a series of articles contributed, by a number of persons on some special topic."

The trouble with this particular symposium is that its special topic was apparently rather vaguely formulated or perhaps not formulated at all. From the title one is led to expect discussions of such questions as "What is a genus?" "How does one define genera?" "Are they synthetic or analytic?" "Are they objective or conceptual?" "Of what use are they to the taxonomist?" "What characters are of value in delimiting genera?" A former symposium on the same subject (Bull. Torrey Club 67: 349–389. 1940) did actually discuss such philosophical questions. But they are left untouched in the present publication, and, indeed, if one searches for a thread upon which to string the separate contributions, one must be content with "New kinds of data in taxonomy," or something like that.

The editor, Frans Verdoorn, does indeed provide a "Foreword" on the need for generic floras—i.e. for catalogues of the genera, rather than the species, of various parts of the earth. And Theodor Just contributes an "Introductory essay" which contains a plea for generic synopses of the larger groups. The first paper, by Lawrence, bears the same title as the entire symposium, and might be expected to outline the problems to be attacked; his subtitle, "The need for an expanded outlook," provides the clue to its content. He exemplifies families and other groups in which differentiation of genera is difficult, and advocates a synthesis of data from all sorts of botanical fields, without venturing to indicate what difference such data might make in taxonomy.

Bailey ("The anatomical approach to the study of genera") regards anatomical data as "another string to the taxonomist's bow," not inherently more reliable than other characters. He gives several examples of the use of anatomy in the classification of genera into families. He is also concerned with the disposition of a number of small "relic" genera. But of the "nature and definition" of genera he says nothing. Eames' paper ("Floral anatomy as an aid in generic limitation") is to much the same effect, except that he apparently regards anatomical characters of flowers as decisive. Much of his discussion is a convincing argument for segregation of *Paeonia* in a distinct family. Rollins ("Cytogenetical approaches to the study of genera") alone deals with the topic

of the title, in taking up the relatedness of species within a genus. Discontinuity between genera may thus be placed on a basis of actual consanguinity; certainly a working basis for the concept of the genus. Cave ("Cytology and embryology in the delimitation of genera") surveys the Liliaceae from the embryological point of view; apparently the conclusions are based on the postulate that "the embryological characters of the species within a genus are constant." Finally Mason ("Plant geography in the delimitation of genera") gives us a valuable discussion of the danger of considering discontinuity, either evolutionary or geographic, apart from the individuals which make up plant groups; taxonomic categories are "incapable of dynamics."

The little book is well printed and embellished by figures illustrating pages from celebrated works on genera; Dr. Verdoorn is to be congratulated, as usual, on the attractive appearance of his publications. It may be well, however, for the modern editor to consider whether one of his concerns is not with the *language* of his contributors. This symposium is marred by a number of grammatical errors and mis-spellings.—H. W. RICKETT.

The Genus Euglena. By Mary Gojdics. viii + 268 pages, 39 plates. University of Wisconsin Press, Madison. 1953. $6.50.

This work of Dr. Gojdics in assembling all the species of the genus Euglena in one book is a welcome addition to the literature for workers in the fields of Phycology, Protozoology and Physiology. The recent experimental work being done in physiology and biochemistry using Euglena makes it essential to have a ready reference to all the species and varieties recognized as valid. Dr. Gojdics' years of work with the genus, both in the field and laboratory, has qualified her for the task of writing this critical monograph.

The general discussion in part one reviews the literature on the morphology and taxonomy of Euglena. It brings together in one volume the basic taxonomic and morphological facts about the genus and in addition reviews the conflicting opinions held in respect to those hypotheses that are still controversial. Dr. Gojdics has not included any of the recent physiological research on the group, and it is the opinion of the reviewer that this is hardly the place for it, as much as such a review is needed.

A complete set of keys to species constitutes part two of the book. The shape and size of chromatophores and paramylum grains are used to separate groups. Since the chromatophores are difficult to observe, directions are given for treatment to expose them clearly.

In part three, each species is described in detail as to size, pellicel, chromatophores, pyrenoid, paramylum, flagellum, reservoir, eyespot, nucleus, cysts and movement. Sources of data are given under each description. Wherever necessary, the description ends with comments about that particular species. Each species and variety is figured.

Part four is an annotated check list of the species of the genus. The thirty-nine plates follow this part of the book. The figures are well drawn and show the diagnostic features referred to in the text descriptions. Credit is given for those drawings taken from other works. The bibliography is ample.

I am certain that students everywhere will welcome this addition to their reference shelf.—E. T. MOUL, Department of Botany, Rutgers University

NOTES

The MANUAL OF THE SOUTHEASTERN FLORA by John Kunkel Small has been taken over by the University of North Carolina Press and will be made available in the original format. This volume, originally published by the author in 1933, has been out of print for some years and this action by the Press will be cordially approved by botanists generally. —J.A.S.

A new periodical has appeared which will interest some readers of the BULLETIN. It is *Acta Phytotherapeutica*, Vol. 1, No. 1, a modest pamphlet of 20 pages measuring 6¼ by 8¼ inches, reproduced from typewritten copy. It contains 9 brief articles; the following titles are representative: "L'Eucalyptus en Algérie"; "Chinese shrub [*Trip-*

terygium wilfordii] seen yielding potent new insecticide''; ''Heilpflanzen gengen Herz- und Kreislaufkrankheiten und deren Folgen''; ''Soya bean source of new edible antibiotic.'' It is published at Keizersgracht 714, Amsterdam—C; the editor is E. F. Steinmetz; the price in the United States is $5.25 for the 10 issues which will appear in a year.—H. W. RICKETT.

The Cultural Branch of the French Embassy (972 Fifth Avenue, New York 21) has recently distributed the first issue of the second series of the French Bibliographical Digest, devoted to biology (including botany and zoology). Pages 35–56 are occupied by references to recent French botanical literature. Perhaps half of these citations are accompanied by abstracts, some of which review the contents of the papers in considerable detail. The issue is distributed without charge to all interested persons.—H.W.R.

Norman Taylor has retired as director of the Cinchona Products Institute in New York, a position he has held for the last seventeen years. The Institute, which has sponsored many research projects in medicine and pharmacology, is suspending its activities in the United States and all correspondence regarding it should be addressed to Cinchona Instituut, 142 de Lairessestraat, Amsterdam—Z, Holland. Mr. Taylor's Address is 20 West 10th Street, New York 11, N. Y.

BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 81, No. 4, pp. 371–385 JULY, 1954

INDEX TO AMERICAN BOTANICAL LITERATURE

COMPILED BY
LAZELLA SCHWARTEN
WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX

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(See also under Morphology: **Gentile & Snell; Sparrow**; under Genetics: **Fischer**)

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